PALYNOLOGICAL CHARACTERISATION OF AMAZONIAN RAINFOREST COMMUNITIES, NORTHEAST BOLIVIA

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DECLARATION

Except where otherwise stated, this thesis, and the data presented therein is entirely the result of my own efforts. This work contains no material that has been accepted for the award of any other degree or diploma in any university or tertiary institution. Except where otherwise stated, and to the best of my knowledge, this work contains no material previously published or written by another person.

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Abstract

An ongoing controversy in Neotropical Palaeoecology is the extent to which Amazonian rainforest communities have responded to climate change over the last glacial-interglacial cycle. One way in which progress can be made in this field is to establish characteristic pollen signatures for different, biogeographically distinct rainforest communities, to compare these with fossil pollen assemblages numerically and thereby extract additional ecological information from the Quaternary sedimentary record. To this end, this thesis aims to (a) improve the identification of abundant rainforest pollen types to a finer taxonomic resolution; (b) provide pollen signatures for four Amazonian rainforest communities of the Noel Kempff Mercado National Park (NKMNP) situated within the Madeira-Tapajós ecoregion based on data obtained from a network of study plots and (c) compare these modern analogue signatures with core-top pollen assemblages recovered from the sedimentary record of lakes within the park.

Descriptive and morphometric methods are used to identify and differentiate key pollen types of the Moraceae family (*Brosimum*, *Helicostylis*, *Pseudolmedia*, *Sorocea* and *Pourouma*) that are well represented in Amazonian rainforest communities of NKMNP. Using multivariate and cluster analyses applied to modern-pollen and floral-biometric data obtained from study plots situated within rainforest communities of the park, it is demonstrated that *terra firme* (well-drained) evergreen, *terra firme* liana, seasonally inundated, and riparian rainforests are readily characterised by their pollen rain. Analogue matching techniques are employed to numerically compare the resulting signatures with core-top pollen assemblages taken

from the Quaternary sedimentary record of two lakes within the park, and of three others situated in the floristically distinct Llanos de Moxos ecoregion. Such comparisons demonstrate that riparian forest communities represent the closest modern analogue for pollen assemblages obtained from surface sediment samples from lakes within NKMNP; however, elements of *terra firme* forests also constitute a significant proportion of these assemblages. There is a clear separation of pollen trap and surface sediment spectra obtained from NKMNP from those obtained from outside the park reflecting floristic differences between rainforests of the Madeira-Tapajós ecoregion and gallery forests of the Llanos de Moxos ecoregion. These results not only provide the potential for much more detailed and reliable Neotropical palaeovegetation reconstructions but also enable the improved estimation of past carbon storage from Amazonian fossil pollen records.

Chapter 1 Introduction

1.1 Introduction

Undisturbed rainforests of the Amazon Basin are among the most species rich tree communities in the world and account for ca.10 % of global terrestrial primary productivity as well as sequestered carbon (Tian et al., 1998; Melillo et al., 1993). Much of the 5.6 million km^2 area they inhabit still remains in a relatively pristine condition and is relatively unaffected by anthropogenic activity. However, changes in rainforest dynamics and composition have recently been measured and attributed to human-induced climate change, post-industrial increases in atmospheric CO_2 concentrations and deforestation (Laurance et al., 2004; Houghton et al., 2000; Phillips et al., 2005; Baker et al., 2005). Further changes to these ecosystems are expected as the impact of anthropogenic climate change takes hold and the interactions between different components of the carbon cycle are better understood (Phillips and Malhi, 2005; Phillips et al 2002; Valdes, 2000).

Understanding the causal mechanisms that underpin the diversity of species represented in tropical forests, as well as the responses of rainforest communities to changes in atmospheric CO_2 concentrations, is a focal point for Neotropical research (Maslin, 2005; Mayle et al., 2004; Phillips and Malhi, 2005). One way in which progress can be made in this field is by recourse to Amazonian Quaternary Palaeoecology whereby past changes in rainforest dynamics can be inferred from pollen assemblages lodged in sedimentary records. The reconstruction of past forest cover has implications not only for our understanding of the sensitivity of Amazonian plant communities to Quaternary environmental change and the causes

and distribution of Neotropical biodiversity (Beerling and Mayle, 2006), but also for the estimation of past carbon storage that will improve our understanding of global carbon cycle dynamics and better constrain global climate models (Valdes, 2000; Cowling et al., 2005; Mayle and Beerling, 2004).

Quaternary palaeoecological studies of lowland Amazonia are still in their infancy and comprise a relatively small number of fossil pollen records obtained from lake, (e.g. Colinvaux et al., 1996; Bush et al., 2004; Van der Hammen and Absy, 1994; Mayle et al., 2000) river (Irion et al., 2006) and oceanic sediments (Haberle, 1997; Haberle and Maslin, 1999) across an area equivalent in size to that of Europe (Fig. 1.1-1). Much controversy is caused by such poor spatial resolution and extrapolation of results across such a large geographic region is commonplace (e.g. Colinvaux et al., 1996; Bush et al., 2004). Moreover, a considerable amount of ecological information is lost because of our current inability to identify pollen grains to species, or even genus level. Vegetation reconstructions are therefore based on the abundance of a few pollen types, are coarsely resolved at the biome scale and can by no means adequately mirror the true beta-diversity (between-habitat diversity) exhibited by Amazonian rainforests. Since the spatial and floristic heterogeneity exhibited by Neotropical lowland rainforests is not well-captured in pollen assemblages of sedimentary records, interpretations of these records have caused considerable debate on the extent to which Amazonian plant communities have responded to Quaternary climate change. In turn, estimates of past carbon storage required by the climate modelling community to test earth-system models are equally imprecise and poorly resolved (Valdes 2000).

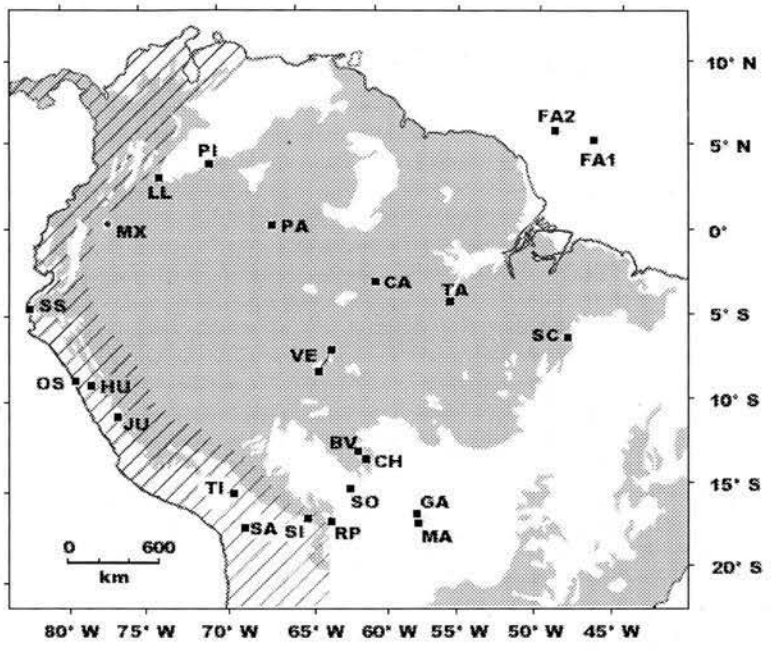

Fig. 1.1-1: Distribution of Neotropical fossil pollen sites in centre-west and northern South America illustrating their low spatial resolution. HU, Huascarán ice-core (Thompson et al. 1995); JU, Lake Junín (Seltzer et al. 2000); TI, Lake Titicaca (Baker et al. 2001); SA, Sajama ice core (Thompson et al. 1998); SI, Siberia (Mourguiart and Ledru, 2003); PI, Laguna El Pinal (Behling and Hooghiemstra, 1999); MX, Maxus 4 (Weng et al. 2002); PA, Lake Pata (Colinvaux et al. 1996); CA, Lago Calado (Behling et al. 2001); VE, Porto Velho (de Freitas et al., 2001); TA, Lago Tapajós (Irion et al., 2006); BV, Laguna Bella Vista (Mayle et al., 2000; Burbridge et al. 2004); CH, Laguna Chaplin (Mayle et al., 2000; Burbridge et al. 2004); SC, Serra dos Carajás (Absy et al. 1991; Sifeddine et al., 2001); FA1, Amazon Fan (Haberle and Maslin, 1999); FA2, Amazon Fan (Maslin and Burns, 2000); GA, Laguna La Gaiba; MA, Laguna Mandioré; SO, Laguna Socorros; RP, Rio Piray (Servant et al. 1981); OS, Ostra (Andrus et al. 2002); SI, Siches (Andrus et al. 2002); Adapted from Mayle et al. (2004).

The central tenet of this thesis is that much of the dispute surrounding the interpretation of Amazonian fossil pollen diagrams may be resolved by improving the taxonomic resolution at which key rainforest pollen types can be identified and by establishing characteristic modern analogue pollen signatures for different rainforest communities. The ability to recognize and identify ecologically important pollen taxa should provide the potential for much more detailed and reliable Neotropical palaeovegetation reconstructions than have hitherto been possible.

Moreover, comparison of modern analogue pollen signatures with fossil pollen assemblages should improve the spatial resolution at which palaeoecological interpretations are made. Adopting an approach that aims to improve Amazonian pollen taxonomy as well as provide modern analogue pollen signatures that represent the heterogeneity of rainforests more realistically, should therefore help resolve much of the debate on the response of Amazonian forest communities to environmental change and provide more precise estimates of past carbon storage.

The key aims of this thesis are a) to differentiate between pollen of the constituent genera of the Moraceae and Urticaceae families which are represented within different kinds of rainforest community in NKMNP; (b) to characterise and differentiate four rainforest communities of NKMNP by their pollen rain; (c) to compare these pollen signatures with floristic inventories numerically in order to understand better pollen-vegetation relationships within rainforest settings and (d) to compare pollen rain spectra with surface sediment pollen samples obtained from the sediment-water interface of 5 lowland lakes to test the applicability of artificial pollen trap data for comparison with the Quaternary sedimentary record.

1.2 Amazonian Palaeoecology

Numerous hypotheses have been put forward to explain the high species diversity and endemism exhibited by different taxonomic groups in the Amazon Basin (Hooghiemstra and van der Hammen, 1998; Colinvaux et al., 2000). The glacial aridity and forest refuge hypotheses (Clapperton, 1993; Haffer, 1969) propose that arid conditions during glacial periods of the Quaternary caused the expansion of savannah ecosystems into the Amazon Basin and the retraction and fragmentation of

rainforest communities into isolated island 'refugia' (Fig. 1.2-1). During interglacial periods, precipitation increased to a sufficient level to support rainforest communities that were able to expand to form a continuous, yet spatially heterogeneous, rainforest cover. According to this theory, the great diversity exhibited by Amazon rainforests today can be explained by allopatric speciation that took place within isolated forest refugia during arid glacial periods (Prance 1982). Much of the empirical evidence that supports this hypothesis comes from the present distribution of endemism of avifauna in Amazonia (Haffer, 1969, Haffer and Prance, 2001) as well as controversial geomorphological evidence of previously active aeolian landforms (Ab'Saber, 1977, 1982). The latter consists of evidence for past sand dune formation underlying contemporary wetlands in regions such as the Brazilian and Bolivian Pantanal and the Venezuelan Llanos (Roa, 1980). Further geomorphic evidence for an arid glacial period includes buried stonelines near Manaus in Brazil, the presence of arkosic sands in the Amazon Fan and gaps in sedimentary sequences (Clapperton, 1993). Much of this evidence is poorly dated and more parsimonious explanations for their formation have been provided by Colinvaux et al. (2000) that do not necessitate aridity during the glacial period.

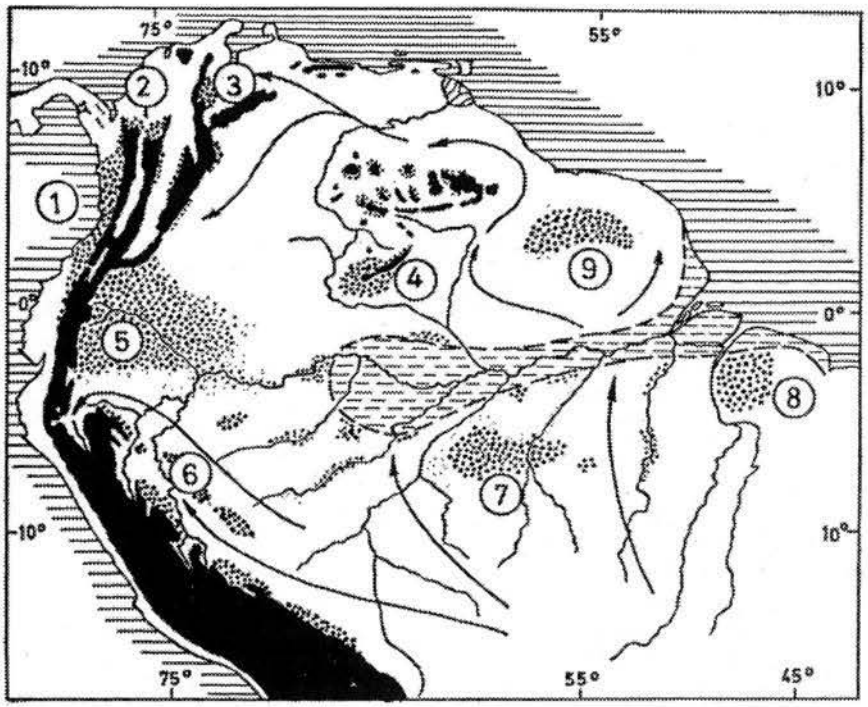

Fig. 1.2-1: Hypothesised rainforest refuges in central and northern South America during glacial periods of the Pleistocene. 1, Chocó refuge; 2, Nechí refuge; 3, Catatumbo refuge; 4, Imerí refuge; 5, Napo refuge; 6, East Peruvian refuge; 7, Madeira-Tapajós refuge; 8, Belém refuge; 9, Guiana refuge; Arrows indicate northward advancing non forest faunas of central Brazil. Source: Haffer (1969).

Little palynological data supports the glacial aridity hypothesis. Evidence supporting the hypothesis includes a pollen record from a lake on the Carajas Plateau (Absy et al., 1991), but the author's conclusions have been subject to considerable scrutiny by Colinvaux et al. (2000, 2001). An increase in the herb to tree ratio recorded at three levels during the last glacial period was initially interpreted to imply expansion of savannah and consequent replacement of forest ecosystems inhabiting the flanks of the plateau. Colinvaux et al. (2000) maintain, however, that the pollen is probably of local origin and that the influx of grass pollen, interpreted by Absy et al. (1991) to have a savannah origin, is more likely to be of aquatic provenance, especially during periods of low lake level when grasses dominate the

littoral zone. Furthermore, Colinvaux et al. (2001) suggest the 'tree component' of the pollen diagram is not indicative of rainforest; instead, it represents disturbance indicator genera including *Cecropia*, *Celtis* and *Trema*, which grow in both rainforest and savannah ecosystems thereby discrediting the interpretations of Absy et al. (1991). Pollen records at Katira Creek in Rondonia (Van der Hammen and Absy, 1994) and from the Noel Kempff Mercado Park in northeastern Bolivia (Laguna Bella Vista and Laguna Chaplin; Mayle et al., 2000; Burbridge et al., 2004) do, however, provide substantial palynological evidence for the replacement of forest with savannah. Nevertheless, Colinvaux et al. (2000) suggest this biome displacement is a result of fluctuations of the forest-savannah ecotone in southern Amazonia and that there is no evidence to indicate that closed-canopy rainforest communities were replaced or fragmented by savannah incursion at a basin-wide scale.

Colinvaux et al. (2000, 2001) suggest that rainforests are inherently stable ecosystems that can withstand significant changes in temperature and precipitation and that remained closed throughout the last glacial period. Indeed, pollen evidence obtained from Lake Pata (Colinvaux et al., 1996) and sediments of the Amazon Fan (Haberle and Maslin, 1999) suggest rainforest cover remained unchanged throughout much of the Quaternary. The rainforest pollen assemblage represented in the fossil record at Lake Pata is consistent throughout. Similarly, rainforest pollen spectra characterise the entire pollen sequence of the Amazon Fan, which is generally considered to be a reliable indicator of Basin-wide changes in vegetation (Mayle and Bush, 2005). In both records, no evidence suggests any long-term variation in either savannah or rainforest taxa apart from the influx of individual Andean taxa that

responded to glacial cooling in the Andes (Haberle and Maslin, 1999; Colinvaux et al., 1996). This 'continuous forest' hypothesis is further supported by terrigenous biomarker and carbon isotope studies (Kastner and Goni, 2003; De Freitas et al., 2001). Analysis of Amazon Fan sediments show constant biomarker and stable carbon isotope concentrations of organic matter deposited between 10 and 70 ka BP (Kastner and Goni, 2003). Moreover, concentrations are similar in composition to those of contemporary alluvial sediments found within rainforest communities and therefore strongly suggest that forest communities of the central Amazon Basin did not change significantly over this time period. Results of carbon isotope studies of soil organic matter along a 200 km transect on the border between Amazonas and Rondonia further demonstrate that the study area was dominated by forest vegetation between 17,000 and 9,000 years BP (de Freitas et al., 2001).

Other evidence supporting the continuous forest cover hypothesis comes from climate and vegetation models (Cowling et al., 2001; Cowling et al., 2006; Mayle et al., 2004; Bonaccorso et al., 2006). Bonaccorso et al. (2006) projected species-specific ecological niche models onto Last Glacial Maximum LGM (ca. 22 Ka BP) climate reconstructions and revealed that their results do not support the broad expansion of savannah species into currently forested areas. Model simulations using biophysical dynamic vegetation models BIOME 3 (Cowling et al., 2001) and BIOME 4 (Harrison and Prentice, 2003) provide further evidence of the persistence of Amazonian forest throughout the Quaternary (Cowling and Shin, 2006). More importantly, simulations run on the University of Sheffield Dynamic global vegetation model (Fig. 1.2-2; Beerling and Mayle, 2006) demonstrate that Amazonian forests not only remain intact across much of the Amazon Basin during

the last glacial period, but are also in agreement with those pollen records that indicate temporal fluctuations in the forest-savannah interface along the Basin's southern and northern margins (Van der Hammen and Absy, 1994; Mayle et al., 2000; Burbridge and Mayle, 2004).

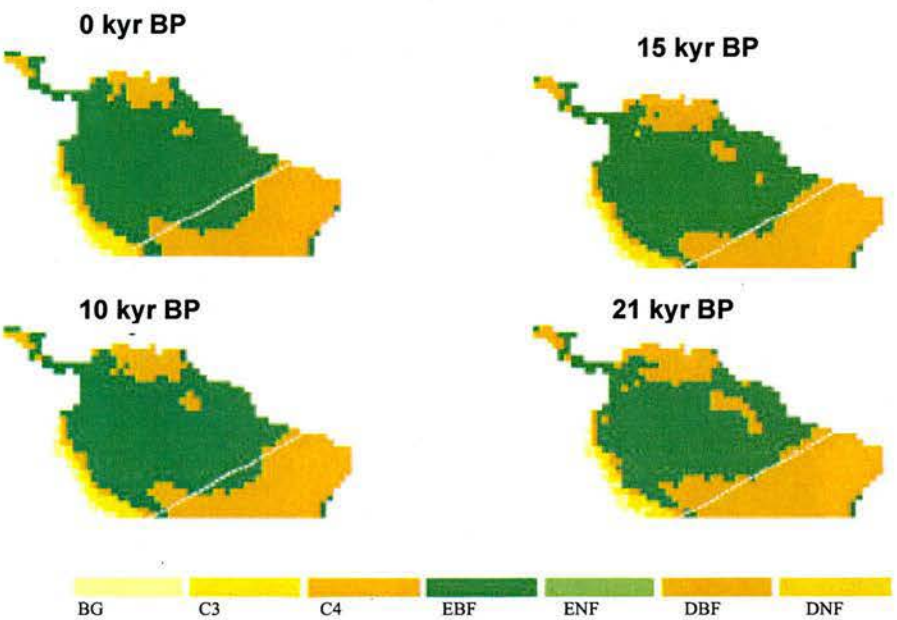

Fig. 1.2-2: Spatial patterns of Amazon ecosystem distribution since the LGM. Amazonia is defined as the area north of the diagonal line. BG, Bare ground; C3, C3 grasslands; C4, C4 grasslands; EBF, Evergreen broadleaf forest; ENF, Evergreen needle leaf forest; DBF, Deciduous broadleaf forest; DNF, Deciduous needleleaf forest. Source: Beerling and Mayle (2006).

While the 'glacial aridity' and 'continuous forest' hypotheses focus on the geographic distribution of forest and grassland communities, the biogeographic importance of other ecologically important plant communities, including semi-deciduous dry forests have, until recently, been ignored (Mayle et al., 2004; Pennington et al., 2000). Indeed, Prado and Gibbs (1993) showed that up to ten disjunct regions of semi-deciduous dry forest can be found distributed across Amazonia (Fig. 1.2-3). They hypothesised that these disjunct communities were once part of a more extensive and continuous dry forest arc that may have reached its

maximum extent during a cool dry period such as the LGM. Furthermore, Pennington et al. (2000) proposed that a matrix of semi-deciduous dry forest dominated the Amazon Basin during the last glacial period and that rainforest and montane taxa were confined to isolated refugia within this matrix allowing allopatric speciation to take place. This model is consistent with all published pollen records but clearly emphasises the equivocal nature of palynological evidence obtained from Amazonian lowland pollen records. Indeed, Pennington et al. (2000) point out that, when operating at such a low taxonomic resolution, up to 80% of fossil pollen types attributed to 'tropical rain forest' taxa, equally characterise 'seasonally dry forest' taxa (e.g. Pleistocene pollen assemblages of Lake Pata in central Amazonia, Colinvaux et al., 1996).

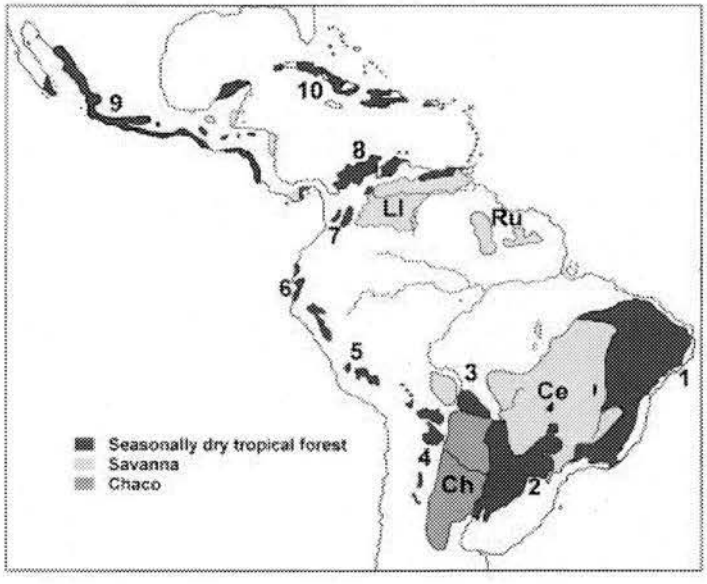

Fig. 1.2-3: The distribution of seasonally dry vegetation in the Neotropics. Seasonally dry forest; 1, Caatingas. 2, Misiones Nucleus. 3, Bolivian Chiquitano region. 4, Piedmont Nucleus. 5, Bolivian and Peruvian InterAndean valleys. 6, Pacific coastal Ecuador. 7, Colombian InterAndean valleys. 8, Caribbean coast of Colombia and Venezuala. 9, Central America. 10, Antilles. Savannas: Ce, Cerrado. Ll, Llanos. Ru, Rupununi. Ch, Chaco. Source: Pennington et al. (2000).

More recently, Cowling et al. (2001) ran palaeovegetation simulations of the lowland Amazon Basin in order to assess the relative importance of glacial climate and atmospheric CO_2 concentrations for vegetation type and structure. Their results not only support the 'continuous forest' hypothesis, but they also showed that leaf area index (LAI), a proxy for canopy density, is very sensitive to changes in climate and atmospheric CO_2. They subsequently put forward the 'canopy density hypothesis', which suggests that variations in the LAI of glacial rainforest communities may have promoted allopatric speciation by the geographic isolation of species in the forest sub-canopy (Cowling et al., 2001). Consequently, these glacial density changes within the forest canopy may explain the great diversity and endemism exhibited in contemporary Amazonia. Such a hypothesis is consistent with the presence of either a glacial dry forest arc (Prado and Gibbs, 1993) or an expansive continuous rainforest (Colinvaux et al., 2000).

The current consensus among scientists is that most of Amazonia remained forested during the last glacial period and that the glacial aridity theory is no longer the overriding paradigm (Mayle et al., 2004). Nevertheless, supporting evidence is certainly not overwhelming and considerable controversy still remains regarding the interpretation of fossil pollen records. Improvements in pollen taxonomy and development of modern analogue studies are essential if more ecological information is to be extracted from these records and the heterogeneity of contemporary rainforest ecosystems is to be captured.

1.3 Neotropical Palynology

The high species diversity exhibited by Amazonian ecosystems, which reaches > 300 species ha^{-1} in western Amazonian rainforest communities (Gentry, 1987), may cause trepidation when rainforest pollen taxa are to be identified. However, pollen trap studies show that a relatively small percentage of rainforest genera are abundant in the pollen rain (Bush and Riviera, 1998; Gosling et al., 2005). The most abundant pollen taxa are dispersed by dioecious anemophilous (wind-pollinated) species of the urticalean rosids Moraceae, Urticaceae, Cecropiaceae and Ulmaceae, which make up a large proportion of a given plant communities' pollen rain and this significantly reduces the pool of pollen types to be identified by the palynologist. Pollen of the Moraceae, Urticaceae and Cecropiaceae families is among the most abundant within Amazonian rainforest pollen spectra and regularly accounts for more than 70% of the total pollen sum (Mayle et al., 2000; Burbridge et al., 2004; Gosling et al., 2005; Irion et al., 2006; Bush et al., 2007). Since urticalean rosids generally exhibit the same anemophilous pollination strategy and their pollen grains are morphologically similar, they have hitherto only been identified to the family level. Indeed, in Amazonian pollen diagrams, the Moraceae pollen category is frequently combined with that of the Urticaceae family due to inability to differentiate between grains of these families (e.g. Colinvaux et al., 1996; Bush et al., 2004; Mayle et al., 2000; Bush et al., 2007). Since genera and species of these families are adapted to a broad range of habitats and pollen can only be identified at the family level, a considerable amount of ecological information is lost when vegetation reconstructions are made from fossil pollen sequences. Improved identification of their pollen to a finer

taxonomic resolution is therefore a priority if more detailed, higher resolution vegetation reconstructions are to be made.

Animal-pollinated (zoophilous) taxa represent ca. 95% of rainforest vegetation and their identification is considerably more difficult and time consuming (Bush et al., 2001; Colinvaux et al., 2000). However, a far more detailed pollen signal may be obtained when they are taken into consideration. Zoophilous taxa generally represent a small proportion of the overall pollen sum because their pollination strategy is not as 'messy' as that of anemophilous taxa. Indeed, zoophily is often a result of the co-evolution of plant and pollinator, which ensures successful pollination and reduces the need for the production of vast amounts of pollen (Bush and Riviera, 1998). Since the pollen is not as widely dispersed as that of anemophilous taxa (i.e. the source area is smaller) and that many of these species are indicator taxa restricted to specific environmental conditions, a more detailed, highly resolved reconstruction of the local flora would be possible if it was identified to a finer taxonomic resolution.

However, only three key Amazonian pollen identification resources are currently available for Neotropical palynologists. Considering the great diversity of species and considerable regional floristic differences within central and southern America these resources are clearly unable to encompass such diversity. Roubik and Moreno (1991) provide a guide to the pollen and spores of the well-studied lowland tropical forest of Barro Colorado Island (BCI), Panama, which is the most comprehensive pollen flora of Neotropical forests to date. The vegetation of central Panama shares ca. 82% of woody plant genera and 21% of species with lowland Peruvian rainforests of the Amazon Basin and has broad affinities with lowland flora

of central and southern America. Since pollen can generally only be identified to the genus level, their pollen manual is considered appropriate for use in regions of the Amazon Basin (Roubik and Moreno, 1991). A pollen atlas developed by Colinvaux et al. (1999) draws upon 421 Amazon pollen taxa extracted from sediments in lakes of lowland Amazonian tropical forests. While the illustrated fossil pollen grains are clearly representative of those found within the sedimentary record, the use of fossil pollen material for taxonomic purposes must be questioned. Most recently, Bush and Weng (2007) provide a searchable digital database of > 1000 pollen taxa collected from vouchered herbarium specimens and targeted towards the most prolific pollen producers based on pollination syndrome and flower structure. To date, this is the most comprehensive searchable collection of Neotropical Pollen, which benefits from the contributions of researchers submitting pollen taxonomic information from different geographic regions.

Despite the great value of these taxonomic resources, considerable floristic differences are manifested across the Amazon Basin and reference manuals must therefore be supplemented by local pollen reference collections. Indeed, two strong floristic gradients in tree composition occur across Amazonia (Fig. 1.3-1; ter Steege et al., 2006; Witmann et al., 2006). One spans rainforest communities between the Guiana Shield in northeastern Amazonia and the lowlands of southwestern Amazonia. The second gradient correlates with a slope of dry-season length increasing from northwest to the southeastern margin of Amazonia (ter Steege et al., 2006). As a result of such heterogeneity, the floristic composition of one region of the Amazon Basin is significantly different to that of any other. For example, the ten most abundant rainforest genera of the Guiana shield (*Carapa*, *Lecythis*, *Aldina*,

Pentaclethra, *Alexa*, *Dicorynia*, *Eperua*, *Catostemma*, *Mora* and *Dicymbe*) are predominantly of the Fabaceae (Leguminosae) family and are different from those of western Amazonia (*Iriartea*, *Attalea*, *Otoba*, *Oenocarpus*, *Pseudolmedia*, *Ficus*, *Clarisia*, *Sapium*, *Spondias* and *Cecropia*), which are mainly of the Arecaceae and Moraceae families (ter Steege et al., 2006).

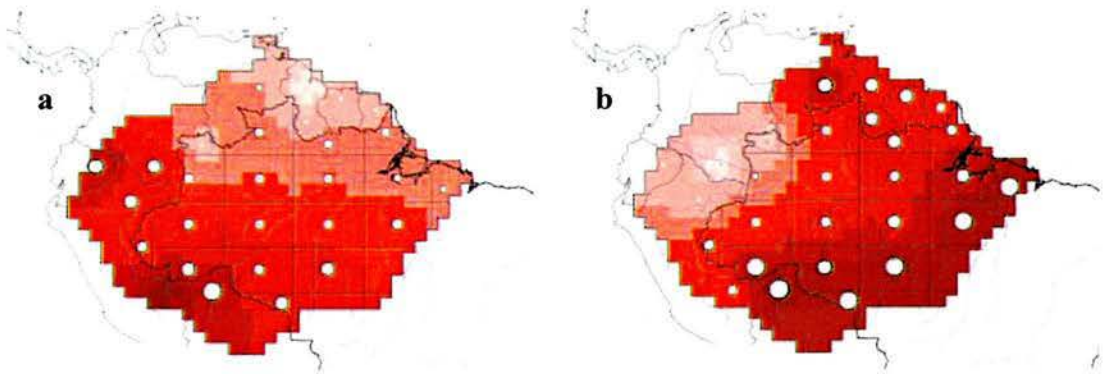

Fig. 1.3-1: Geographic variation in community characteristics of South American tree communities. Values in each region are illustrated by the sizes of the open circles and are based on all individuals in that region; **a**, Scores on the first axis of the gradient analysis (detrended correspondence analysis) of genus-level community composition; **b,** Scores on the second axis of the same analysis. Source: ter Steege et al. (2006).

Considerable floristic differences are also manifested at the beta-diversity level between rainforest communities experiencing different degrees of inundation. *Terra firme* evergreen rainforests are the most species rich comprising well-drained rainforests including drought-adapted liana forests as well as moist evergreen rainforest communities. Flooded forests are periodically inundated by igapó (blackwater) and várzea (whitewater) rivers that drain the Precambrian Shield and the Andes mountains, respectively (Sioli 1968; Prance 1979, 1989). In terms of diversity and physiognomy, seasonally-inundated and riparian forest communities are notably less species-rich and constituent trees are generally shorter than those in *terra firme* forests (e.g. Duivenvoorden, 1996; Nebel et al., 2001), reflecting their

more temporary nature as they respond to hydrological changes of meandering Neotropical rivers. Furthermore, numerous genera are highly specialised and adapted to specific levels of inundation. Of the Moraceae family, for example, the várzea tree *Maquira coriacea* is restricted to, and regularly dominates, flood plain forests of the Amazon, Orinoco and upper Rio Paraguay Basins (Nebel et al., 2001). In contrast, *Helicostylis tomentosa* flourishes in well-drained (*terra firme*) tall evergreen rainforests and liana forests (Killeen, 1998). The shrub *Brosimum gaudichaudii* prefers rather more arid environments and grows in both open woodland and *cerrado* (well-drained savanna) communities along the southwestern margin of the Amazon Basin (De Oliveira-Filho, 1992; Marchant et al., 2002). In order to capture these floristic differences within the pollen rain and to aid the identification of pollen of anemophilous and zoophilous plant taxa, it is therefore imperative that local pollen reference collections are prepared to supplement the pollen manuals described above.

1.4 Modern pollen-vegetation studies

The reconstruction of past floras using pollen analysis of Quaternary sediments has always been a difficult and complex problem (Birks and Gordon, 1985). Not only is a deep knowledge of contemporary ecology required, but there is also a need to understand the relationships better between modern pollen spectra and the taxonomic composition of the vegetation from which the pollen is derived (Birks and Gordon, 1985). In temperate regions, modern pollen studies have substantially improved interpretations of fossil pollen records since the 1950s (e.g. Fagerlind, 1952; Davis, 1963; Hicks and Birks 1996; Huntley, 1996; Bennet and Hicks, 2006). When compared with pollen studies from higher latitudes, the considerable diversity and

species richness exhibited by Neotropical rainforests introduces a much greater complexity into the study of pollen-vegetation relationships. Such complexity is poorly understood due to the dearth of modern pollen studies available (Bush and Riviera, 1998, 2001; Gosling et al., 2005; Behling and Negrelle, 2006).

One approach, adopted in part by Bush and Riviera (1998, 2001) and Gosling et al. (2005), is to estimate pollen-representation factors for each individual species, which quantify the relationship between pollen abundance and that of species in the surrounding vegetation. These representation factors can subsequently be used to estimate the past abundance of taxa based on pollen assemblages obtained from the fossil record. Indeed, Bush and Riviera (2001) drew an important conclusion from a three year study of pollen rain data from a lowland rainforest on Barro Colorado Island, Panama. In general, the authors showed that dioecious and anemophilous taxa were over-represented in pollen spectra when compared with floristic data. Moreover, their study suggested that pollen spectra in lake sediments are most likely to consist of these over-represented pollen types and that plants exhibiting closed-flower pollination syndromes will be under-represented in the fossil record. Gosling et al. (2005) derived similar results from the analysis of a *terra firme* (well-drained) moist evergreen forest in northeastern Bolivia. While useful, the calculation of pollen abundance in these studies is fraught with large calculation errors associated with the addition of a spike of exotic pollen (Maher, 1981; Stockmarr, 1972). Furthermore, both these investigations are based on pollen rain obtained from just one vegetation plot despite many studies suggesting that a taxon's representation factor may vary between sites (Birks and Gordon, 1985). Other simplifying assumptions regarding the extent of the pollen source area around the site under investigation need to be

made if the representation factor approach taken, many of which are associated with considerable uncertainty (Birks and Gordon, 1985). Indeed much criticism has engulfed the study of pollen-representation factors, which is discussed at great length in Birks and Gordon (1985).

In view of these constraints, it seems prudent for Neotropical palynology to adopt a 'comparative approach' (*sensu* Birks and Gordon, 1985) and deal, in the first instance, with the final product of a plant communities' pollen productivity: the modern pollen spectrum. Pollen spectra may be obtained by the analysis of pollen obtained from a network of pollen traps (natural and synthetic) within a particular plant community. Trapping media are variable but the most common are moss polsters (Weng et al., 2004; Waller et al., 2005; Pardoe, 2006), soil samples (Elenga et al., 2000; Vincens et al., 2000) and synthetic pollen traps (Bush and Riviera, 1998; Bush et al., 2001; Gosling, 2003; Gosling et al., 2005). The recovery of consistent modern pollen signatures from multiple plots within each plant community under investigation may then provide a collection of representative 'modern analogue spectra' with which fossil pollen assemblages may be compared. Such an approach has the added benefit of operating at the beta-diversity (plant community) scale enabling the realistic comparison of pollen and floristic data. Furthermore, the provision of a database of pollen signatures that represent different habitats will eventually permit the development of transfer functions that relate contemporary pollen assemblages to measured environmental variables. Assuming these transfer functions are invariant through time, they may then be used to estimate environmental variables from fossil pollen assemblages obtained from the sedimentary record (Birks and Gordon, 1985).

Very few modern pollen-vegetation studies exist in tropical latitudes of South America. However, pollen trapping studies performed in dense forests in South Congo in Africa have demonstrated a strong relationship between pollen rain spectra, obtained from modern soil samples and the surrounding vegetation (Elenga et al., 2000). Using multivariate and cluster analysis the authors demonstrate that swamp forests can be readily differentiated, both floristically and palynologically, from those developed on well-drained soils. Moreover, they were also able to palynologically distinguish forests growing on sandy soils and those growing on ferralitic soils. Thus, floristic heterogeneity exhibited by different forest communities and controlled by underlying edaphic and hydrological constraints was well-captured by the forests' pollen rain. Similar conclusions were drawn by Vincens et al. (2000) who analysed modern soil and litter samples along a rainforest-savannah transect in southeastern Cameroon and demonstrated that forest ecosystems can be readily differentiated from savannah ecosystems by their pollen spectra. Both studies suggest that the beta-diversity exhibited by tropical ecosystems is well manifested in pollen rain assemblages; however, neither compares the resultant modern pollen spectra with fossil pollen assemblages to test the effects of different depositional environments on the resulting fossil pollen assemblage. In order to extract such high resolution ecological information from the sedimentary record, taphonomic differences between depositional environments need to be taken into account. Factors affecting the resulting pollen signature may include geographic location, catchment size, basin morphometry, geology, aspect and topography, the presence or absence of aquatic vegetation and human influences (Moore et al., 1991). Since modern pollen-vegetation studies are designed to improve the interpretation of fossil pollen records,

it is essential that pollen rain spectra are directly compared with surface sediment assemblages within the same plant community to test for the relative impact of taphonomic processes on resulting pollen assemblages. Unless such comparisons are made, the application of pollen-vegetation studies to fossil pollen records will remain problematic.

Within the Amazon Basin, previous pollen-vegetation studies have shown that Andean montane forests may be palynologically differentiated from lowland forests (Behling et al., 1997; Bush 1991; Islebe and Hooghiemstra, 1997; Rodgers and Horn, 1996), savannahs separated from lowland forest (Salgado-Labouriau, 1997; Gosling et al., 2004) and morichal (palm swamp forest) separated from *terra firme* forest (Behling and Hooghiemstra, 1999). Bush et al. (2001b) examined the influence of beta and gamma-diversity (regional species turn-over) on modern pollen rain obtained from rainforests near Manaus, Brazil and from Cuyabeno in Equador. Multivariate analyses confirmed that beta-diversity is well captured by the pollen rain, particularly in the presence of strong underlying environmental gradients such as an inundation gradient. Importantly, gamma-diversity actually produced a stronger signal within the pollen than did beta-diversity, a result that is consistent with basin-wide geographic floristic gradients exhibited across Amazonia (ter Steege et al., 2000).

In order to improve the interpretation of Neotropical fossil pollen records within the Noel Kempff Mercado National Park (NKMNP), northeastern Bolivia, Gosling (2004) utilised a variety of bivariate and multivariate statistical techniques to characterise and differentiate successfully between *terra firme* evergreen forest, *terra firme* savannah and semi-deciduous dry-forest communities by their modern pollen

spectra, which were obtained from a series of one-hectare plots within the park. Pollen rain spectra were subsequently compared with surface samples recovered from lakes surrounded by each of the studied plant communities to test for the influence of taphonomic processes on the resulting fossil pollen spectrum. Surface samples obtained from lakes within semi-deciduous dry forests were shown to be distinct from those of *terra firme* evergreen forest and savannah lakes, which were in turn distinct from each other. These samples were also shown to be congruent with pollen trap samples obtained from the same plant community. Only relatively high levels of aquatic grass pollen found within lake sediments skewed the pollen spectra away from that of the pollen rain. Following removal of aquatic pollen from sediment pollen assemblages, modern pollen rain data were subsequently shown to be comparable with the fossil pollen record (Gosling et al., 2005).

1.5 Thesis rationale, site description and methodology

1.5.1 *Rationale*

The ability to differentiate between pollen spectra of different rainforest communities is essential if more detailed palaeoecological reconstructions are to be made within the lowlands of tropical Amazonia. For example, if a given fossil rainforest pollen assemblage is demonstrably of a riparian forest provenance, this would imply that the sedimentary record only records a local riparian rainforest signal. In contrast, if such an assemblage was shown to be of a *terra firme* upland forest provenance, this would reflect pollen deposition from well-drained forested areas distant from the shoreline. Such a distinction is of particular importance for our understanding of glacial fossil pollen assemblages recorded in sediments of the Amazon Fan (Haberle 1997;

Haberle and Maslin, 1999) and at Lake Pata (Colinvaux et al., 1996). A *terra firme* moist forest pollen signal recorded in these sediments would reflect spatially more extensive upland rainforests and be consistent with the continuous forest hypothesis of Colinvaux et al.(2000). If these assemblages were shown to be of riparian forest provenance, they would be representative of flooded forest communities lining the rivers of the Amazon Basin, which mask pollen derived from other plant communities beyond. This would be consistent with the glacial aridity hypothesis (Haffer, 1969; Prado and Gibbs, 1993; Van der Hammen and Absy, 1994; Haffer and Prance, 2001; Pennington et al., 2000). The palynological differentiation of liana rainforest communities also has implications for palaeoecological interpretations. Lianas have an adaptive advantage over trees with regard to water transport, which leads to the dominance of this life form on landscapes where seasonal drought and dystrophic soils dominate (Killeen, 1998; Phillips et al. 2002). These forests exhibit lower biomass than tall moist forest communities. Evidence of liana forest expansion within the palaeoenvironmental record could therefore point to changes in soil water availability as well as periods of lower CO_2 sequestration.

Each of the above mentioned forest communities are well represented in the Noel Kempff Mercado National Park (NKMNP), a 15,230 km^2 biological reserve situated in the tropical lowlands of northeast Bolivia, which forms the principal study area for this project.

1.5.2 *Study Area*

NKMNP occupies part of the Madeira-Tapajós ecoregion (Fig. 1.5-1; Olsen et al., 2001). The park is situated on an ecotone spanning 22 plant communities, from moist

evergreen rainforest in the north, to *cerrado* (well-drained savanna) in the east, and semi-deciduous dry-forest communities in the south, and provides a physical setting that supports considerable ecosystem diversity (beta diversity; Killeen et al., 2002). Two black-water rivers, the Río Iténez and Río Paraguá define the eastern and western boundaries of NKMNP, respectively. Precambrian rocks of the Huanchaca Plateau (600-900 m a.s.l.) characterise the eastern half, and Tertiary alluvial deposits of the lowland peneplain (200-250 m a.s.l.), the western half of the park. The vegetation of the Huanchaca Plateau consists mainly of *cerrado* savanna communities, which are adapted to well-drained soils overlying the basement rocks of the Precambrian Shield. Here, moist evergreen gallery forest is confined to valleys or depressions where water availability is sufficient for forest development (Killeen, 1998). In contrast, a variety of evergreen rainforest communities dominate the neighbouring alluvial plains. High evergreen rainforest and liana forest grow on well-drained (*terra firme*) soils, while riparian and seasonally inundated rainforests, as well as seasonally flooded savannas, develop on hydromorphic soils formed by alluvial deposition during overbank flow of the Río Paraguá in the wet season (October – March). Fossil pollen analyses of sediments from the two large lakes in NKMNP, Laguna Chaplin (14° 28' S, 61° 04' W) and Laguna Bella Vista (13° 37' S, 61° 33' W), have revealed changes in vegetation, fire dynamics, and climate, over the last 50,000 years (Burbridge et al., 2004; Mayle et al., 2000).

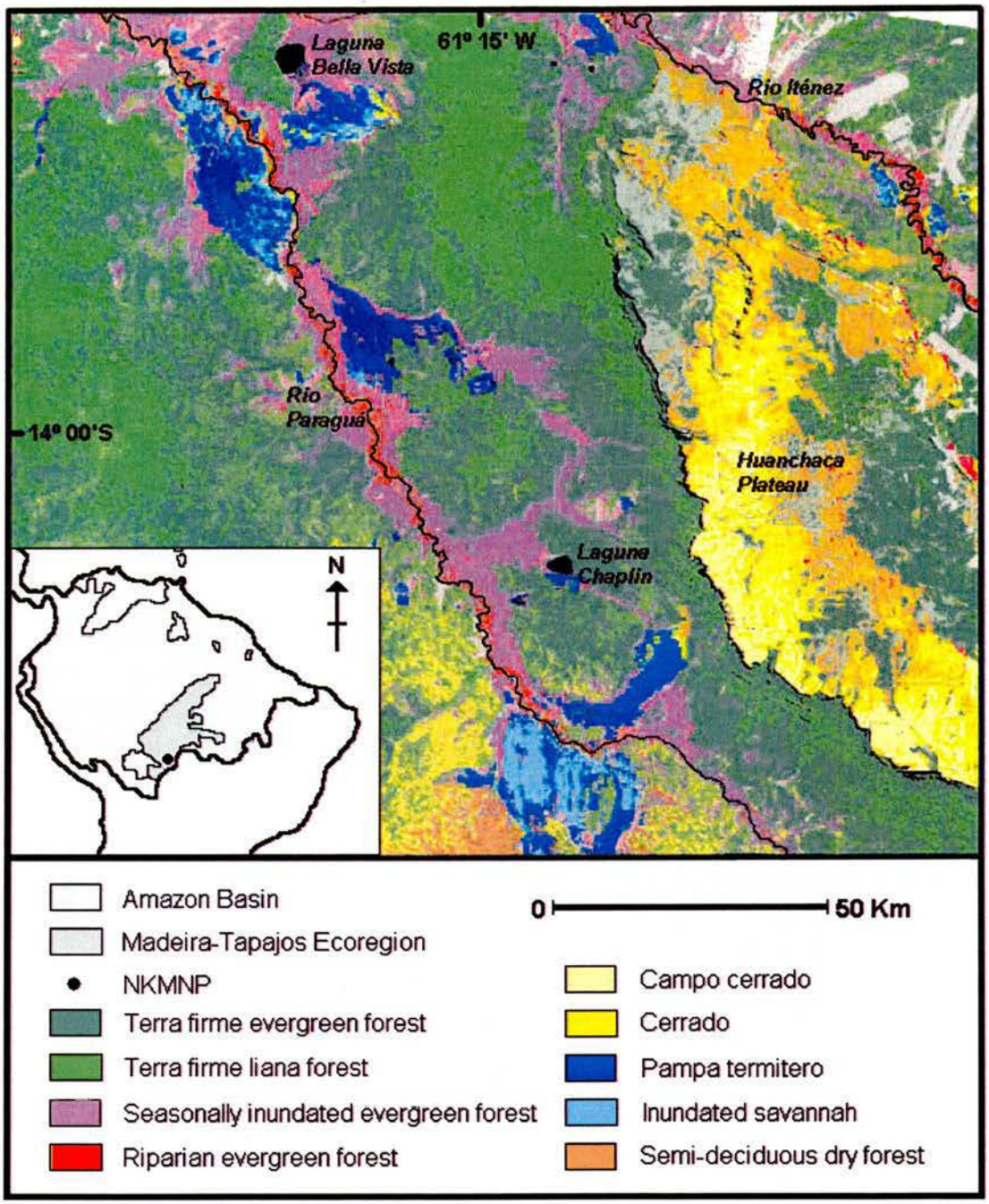

Fig. 1.5-1: Location map (inset) and distribution of plant communities within Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. Modified from Killeen and Schulenberg (1998).

1.5.3 *Methodology*

1.5.3.1 Delineation and definition of four studied plant communities

Terra firme moist evergreen rainforests of the NKMNP grow on red, well drained and deep Oxisols (Soil Survey Staff, 2008) that have developed on ancient Tertiary alluvial material, estimated to be 6 to 20 million years old (Killeen, 1998; Fig. 1.5-1). These soils are deep and strong enough to support forests with a tall structure where tree heights up to 45 m and trunk diameters of 1.5 m are common. *Pseudolmedia laevis* is the most abundant canopy tree in this forest and emergent trees including *Qualea paraensis*, *Erisma gracile*, *Apuleia leiocarpa* and *Moronobea coccinea* are well represented. *Phenakospermum guianense* tends to form colonies and is only sporadically abundant. Palm trees including *Attalea maripa* and *Astrocaryum aculeatum* are abundant and *Euterpe precatoria* and *Socratea exorrhiza* are more common on more poorly drained soils.

Terra firme evergreen liana forests occupy higher ground within the park (Fig. 1.5-1) and grow not only on well-drained, dystrophic oxisols that have developed on Tertiary sediments but also on low mountain ridges composed of quartzite rocks. They are characterised by a low and dense canopy, which is dominated by the liana growth form and are spatially extensive within the park as well as the Madeira-Tapajós moist forest ecoregion (Olsen et al. 2001). The structure of this forest is homogeneous and is distinguished from *terra firme* moist evergreen rainforest by a low canopy height of ca. 4m, which is also readily differentiated using Landsat imagery (Killeen, 1998). The floristic composition of evergreen liana forests is dominated by species typical of secondary forests including *Cecropia* spp., *Schizolobium amazonicum*, *Apeiba tibourbou*, *Didymopanax morototoni* and *Cordia*

alliodora. The most common palms are *Attalea maripa* and *Astrocaryum aculeatum*. Lianas have an adaptive advantage over other life forms in terms of water transport (Phillips et al. 2003) and are particularly prominent in landscapes that experience seasonal drought as well as dystrophic soils. Semi-deciduous dry forests that occupy the southernmost limits of the park are equally adapted to seasonal drought; however, these forests tend to develop on mesotrophic soils.

Riparian and seasonally inundated forests of NKMNP develop on hydromorphic entisols formed under a very rapid and dynamic depositional environment associated with seasonal flooding of Río Paraguá and Río Iténez (Fig. 1.5-1). Riparian evergreen forests occur as narrow strips of forest on slightly higher ground associated with natuaral levees that line these rivers. Pioneer species such as *Cecropia* spp., *Sapium* and *Acacia* as well as the more established trees of the Moraceae family including *Brosimum lactescens*, *Sorocea guilleminiana* and number of species of *Ficus* are well represented. The understory of these riparian forests is characteristically sparse because seasonal flooding creates an anoxic environment within which few species can survive (Killeen, 1998). Trees that are well-adapted to flooded conditions such as *Maquira coriacea* (Moraceae), *Hevea brasiliensis* (Euphorbiaceae) and *Macrolobium acaciafolium* (Fabaceae) dominate these communities.

Seasonally inundated forests occupy hydromorphic entisols that have developed within extensive floodplains of the park (Fig 1.5-1). Microtopographical variability within this inundated landscape provides the opportunity for the growth of tall forest taxa as well those adapted to seasonal inundation, which, in turn, increases the structural and compositional diversity of this forest community. Shrubs and small

trees of the Melastomataceae family, including the invasive *Miconia*, are common and well adapted to areas exhibiting more open conditions; however, tall canopy trees including *Brosimum*, *Maquira*, *Sorocea* and *Ficus* of the Moraceae family are equally well represented.

1.5.3.2 Floristic Sampling

Detailed floristic inventories of the studied plant communities were obtained from one-hectare, rectangular permanent study plots (500 × 20 m) between 1993 and 2000 by Killeen (1998) and are readily available from the Salvias Project Database (2007). Two plots were set up for each of the studied communities and installed in visually homogeneous forest according to Landsat imagery in order to minimize intra-plot heterogeneity. Soil parent material is an important control on the structure and composition of different plant communities and ground-based reconnaissance was performed to ensure homogeneity of soil for a given pair of plots within the same plant community. Every woody plant ≥ 10 cm d.b.h. (diameter at breast height) was measured and all tagged specimens were stored at the herbarium of the Museo de Historia Natural Noel Kempf Mercado in Santa Cruz, Bolivia. Identification was made by comparison with specimens held in the collection in Santa Cruz and at the Missouri Botanical Gardens (Killeen and Schulenberg, 1998). Standardized nomenclature is in accordance with publications cited in the International Plant Names Index (2007), a combination of Index Kewensis, the Gray Card Index and the Australian Plant Names Index. Our study employs floristic data obtained from eight of these plots situated within four different rainforest communities.

One hectare inventories are routinely used by botanists to infer ecological patterns at local, regional and continental scales and are often converted into long-

term plots to monitor forest processes (Phillips et al. 2003). An alternative method developed by Gentry (1982) involves sampling all stems ≥ 2.5 cm diameter in ten 0.01 ha transects each of 2 × 50 m. The advantages of the former sampling strategy include lower sampling error for a given plot (since the area is larger) and a focus on plants which contribute > 90% biomass.The main advantages of the latter method are that it includes smaller species and stem sizes, provides relatively rapid replication across the landscape and is practically efficient in terms of time spent in the field (Phillips et al. 2003). In NKMNP, rectangular plots of 500 × 20 m were selected in order to intercept the largest possible number of micro-habitats so that species richness was well captured (Killeen, *pers comm*). Indeed, Condit et al. (1996) found that rectangular plots of 500 × 20 m yielded 5.3-11.3 % more species than square plots of equal area in rainforest communities in Malasia and Barro Colorado Island, Panama. Moreover, rectangular plots will be less susceptible to 'mature forest' bias and single tree fall events will have less influence on the overall floristic composition (Phillips et al. 2003).

The extent to which floristic information based on two 1-ha plots is representative of regional forest composition needs further study and extrapolation of results should therefore be performed with caution. Nevertheless, compositional similarity between plots provides a degree of confidence that the studied plots are representative of distinctive plant communities within the park. Moreover, results are regionally consistent at the family and generic level with floristic data obtained from Peru, Bolivia and Brazil (summarised in ter Steege et al. 2006).

1.5.3.3 Taxonomy

A summary of floristic composition of key taxa > 1% cover of each of the studied forest communities is given in Table 3.5-1 (Chapter 3). Voucher specimens are available at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia. Species identification was made by comparison with specimens at this museum as well as at the Missouri Botanical Garden with the assistance of many family specialists. Primary data from the voucher collections, taxonomic authors, and synonyms are available from the TROPICOS database at the Missouri Botanical Garden (TROPICOS, 2008). Clearly, misidentification of species may affect the floristic characterisation of both floristic and palynological datasets. Most misidentifications of plants tend to occur at the species level within genera that are particularly speciose (ter Steege et al. 2006). All numerical analyses performed here are made at the genus level for two reasons. First, ca. 95% of Amazonian taxa are correctly identified at the genus level providing confidence in obtained results (ter Steege et al. 2006). Second, pollen grains can generally only be identified to the genus level. Since numerical analyses require the comparison of botanical and pollen data at the same taxonomic resolution, operating at the generic level is therefore the only logical approach.

The analyses of floristic and palynological data were based entirely on the abundance of species recorded in the floristics inventories and counts of pollen taxa obtained from a series of pollen traps situated within each of the studied plant communities (See Chapter 3). Since the Moraceae family was particularly well represented in both floristic and pollen datasets and that the pollen of this family has not hitherto been separated taxonomically, this family was selected for a study on the

identification of its constituent genera based on those species represented within NKMNP (Chapter 2).

1.5.3.4 Numerical Analyses

Prior to numerical analysis, all data matrices obtained from floristic inventories, pollen trap and surface sediment counts were square-root transformed in order to minimize the effect of over-represented taxa and to optimize the 'signal' to 'noise' ratio (Birks, 1986; Prentice, 1980). Proportional values were used in all cases because they stabilize the variance in the data (Birks and Gordon, 1985; Bennet and Hicks, 2005). Relative density ((number of individuals of species/total number individuals)*100) was calculated for each species represented within the floristic inventory of the studied rainforest plots. Species were subsequently ranked in order of decreasing importance according to their relative abundance. Similarity between taxon assemblages of different plots was measured using the robust and widely applied metric coefficient of squared Euclidean distance (Oksanen et al., 2007; Kent and Coker, 1994). These distances were chosen because they are easily represented in geometric space in ordination analyses (e.g. Principal Components Analysis) and are ecologically meaningful for the analysis of sites representing short ecological gradients (Legendre and Gallagher, 2000; Lepš and Šmilauer, 2003).

Multivariate and cluster analysis was applied to investigate the major gradients of variability in both the vegetation and pollen rain datasets and to group distinct rainforest communities and pollen assemblages into classes according to their taxonomic composition. Data were first analysed using Detrended Correspondence Analysis (DCA) to measure the gradient length in community composition (beta-diversity). Both datasets exhibited a gradient length of less than

two standard deviation units, so the linear unconstrained Principal Components Analysis (PCA) was deemed to be sufficient for subsequent analyses. A PCA was applied to each of the covariance and correlation matrices of floristic and pollen datasets, to detect any structure or patterns within them and to assess the relative contribution of important taxa to the variance in the datasets. Classification of the data was performed using the Unweighted Pair Group with Arithmetic Mean (UPGMA) agglomerative classification technique, an algorithm that iteratively fuses the two nearest clusters (or group of species) until only one cluster remains (Sneath and Snokal, 1973). Here, fusion between clusters is based on the smallest mean pairwise Euclidean distance between taxa.

The extent to which the structure in the pollen rain data is controlled by the distribution of species within the surrounding rainforests was investigated using direct ordination by means of canonical correspondence analysis (CCA; ter Braak 1986). Within a CCA the ordination axes are related to linear combinations of the explanatory variables (i.e. species recorded in floristic inventories) and variance in the pollen rain data is therefore constrained by the distribution of species within the studied forest plots. The species used to constrain the pollen data were selected according to their importance in driving the differentiation of plots as determined by results of PCAs on the covariance matrices of both floristic and pollen datasets. Datasets were harmonized to the same taxon list and the statistical significance of the relationship between selected trees and pollen rain was assessed using a permutation test (Oksanen et al. 2007).

1.6 Summary

An ongoing controversy in Neotropical Palaeoecology is the extent to which rainforest communities have responded to climate change over the last glacial-interglacial cycle. This debate not only hampers progress in our understanding of Quaternary vegetation dynamics, but also in the testing of climate and earth-system models and in obtaining improved estimates of past carbon storage. One way in which progress can be made in this field is to establish characteristic pollen signatures for key rainforest communities, to compare these with fossil pollen assemblages numerically and thereby extract additional ecological information from the Quaternary sedimentary record. To this end, this thesis aims to develop pollen-vegetation studies within the Amazon Basin to distinguish, palynologically, between rainforest communities that are structurally and floristically distinct from each other. In particular this thesis aims to (a) improve the identification of abundant rainforest pollen types to a higher taxonomic resolution; (b) provide pollen signatures for four Amazonian rainforest communities of the Noel Kempff Mercado National Park (NKMNP; Fig 1.6-1) based on data obtained from a network of study plots and (c) compare these modern analogue signatures with core-top pollen assemblages recovered from the sedimentary record of lakes within the park and gallery forests of the Beni Basin (Llanos de Moxos ecoregion; Fig. 3.3-2).

To this end, this thesis is written in journal format and divided into two key papers and a final discussion chapter. The first paper aims at improving the taxonomy of Moraceae pollen found within rainforest communities of the Noel Kempff Mercado National Park. The mulberry family (Moraceae) comprises ca. 37 genera and over 1100 species worldwide and is one of the most abundant and

ecologically important families growing in tropical rainforests of Central and South America (Datwyler and Weiblen, 2004). In general, Moraceae plants are monoecious or dioecious trees and shrubs, and are adapted to a wide range of moist tropical evergreen forest habitats including well-drained *terra firme* forest, liana dominated forest, as well as seasonally inundated and riparian forests (Killeen, 1998). Moraceae/Urticaceae type pollen regularly accounts for >70% of total pollen counts and is considered to indicate the presence of closed-canopy lowland tropical rain forest communities when pollen abundance is > 30% (Mayle et al., 2004; Gosling et al., 2005). Since little work has been done to identify constituent pollen types to a finer taxonomic resolution, the first paper presents the first detailed analysis of the morphological properties of Moraceae and Urticaceae pollen grains of the Amazon Basin. Using descriptive and morphometric methods it attempts to differentiate between pollen of the constituent genera of the Moraceae and Urticaceae families represented within different kinds of rainforest community in Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. In particular, it aims to provide a pollen-taxonomic key that can be used by Neotropical palynologists to identify Moraceae and Urticaceae genera and species.

The second paper presents the first multivariate analysis of pollen rain sampled from permanent plots situated within four rainforest communities of NKMNP, which represent two *terra firme* (moist evergreen rainforest and liana rainforests) and two flooded rainforests (seasonally inundated and riparian forests). The paper aims to palynologically characterise and differentiate all four rainforest communities in order to improve Neotropical palaeoecological interpretations by providing a set of modern analogue pollen spectra to which fossil pollen assemblages

may be compared. The specific aims of the paper are (a) to characterise and differentiate four distinct rainforest communities by their pollen rain captured by a network of 35 pollen traps situated within 8 permanent study plots of NKMNP; (b) to numerically compare these pollen signatures with floristic inventories obtained from the surrounding forests to better understand pollen-vegetation relationships within a rainforest setting; and (c) to numerically compare pollen rain spectra with surface sediment pollen samples obtained from the sediment-water interface of 5 lowland lakes to test the applicability of pollen trap data for comparison with the Quaternary sedimentary record.

The final chapter reiterates the principal aims, results and conclusions of this thesis and places these in the wider context of Amazonian palaeoecology; in particular, it examines wider palaeoecological implications for the Amazon Basin as a whole, discusses underlying assumptions and provides suggestions for future research.

1.7 References

Ab'Saber, A.N. (1977). Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais do Quaternário. Paleoclimas **3**, Instituto de Geografia, Universidades de São Paulo, São Paulo, Brasil, 1–19.

Ab'Saber, A.N (1982). The paleoclimate and paleoecology of Brazilian Amazonia. In: Prance, G.T. (Ed.), *Biological Diversification in the Tropics*, Columbia, New York.

Absy, M. L., Cleef, A., Fornier, M., Servant, M., Siffedine, A., Da Silva, M. F., Soubies, F., Suguio, K., Turcq, B., and Van der Hammen, T. (1991). Mise en evidence de quatre phases d'ouverture de la forêt dense le sud-est de l'Amazonie au cours des 60 000 dernieres années. Première comparaison avec d'autres régions tropicales. *C.R. Acad.Sci.Paris.* **313,** 673-678.

Andrus, C. F. T., Crowe, D. E., Sandweiss, D. H., Reitz, E. J. & Romanek, C. S. (2002). Otolith δ18O record of Mid-Holocene sea surface temperatures in Peru. *Science* **295**, 1508–1511.

Baker, P. A., Seltzer, G. O., Fritz, S. C., Dunbar, R. B., Grove, M. J., Tapia, P. M., Cross, S. L., Rowe, H. D., and Broda, J. P. (2001). The History of South American Tropical Precipitation for the past 25,000 years. *Science*, **291**, 640-643.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Natalino, J., Silva, M. and Martinez, R.V. (2005). Late twentieth-century trends in the biomass of Amazonian forest plots. In: Y. Malhi and O. Phillips (Eds.): *Tropical Forests and Global Atmospheric Change*. Oxford University Press, Oxford.

Beerling, D. J. and Mayle, F. E. (2006). Contrasting effects of climate and CO_2 on Amazonian ecosystems since the last glacial maximum. *Global Change Biology* **12**(10): 1977-1984.

Behling, H., and Hooghiemstra, H. (1999). Environmental history of the Columbian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. *Journal of Paleolimnology* **21,** 461-476.

Behling, H., Keim, G., Irion, G., Junk, W. and Nunes de Mello, J. (2001). Holocene environmental changes in the Central Amazon Basin inferred from Lago Calado (Brazil). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **173**, 87-101.

Behling, H., and Negrelle, R. R. B. (2006). Vegetation and pollen rain relationship from the tropical Atlantic rain forest in southern Brazil. *Brazilian Archives of Biology and Technology* **49,** 631-642.

Behling, H., Negrelle, R. R. B., and Colinvaux, P. A. (1997). Modern pollen rain data from the tropical Atlantic rain forest, Reserva Volta Velha, South Brazil. *Review of Palaeobotany and Palynology* **97,** 287-299.

Bennett, K. D., and Hicks, S. (2005). Numerical analysis of surface and fossil pollen spectra from northern Fennoscandia. *Journal of Biogeography* **32,** 407-423.

Birks, H. J. B., and Gordon, A. D. (1985). Numerical Methods in Quaternary Pollen Analysis.

Birks, H. J. B. (1986). Numerical Zonation, comparison and correlation in Quaternary pollen-stratigraphical data. In BE Berglund (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*: 743-774. John Wiley: Chichester.

Burbridge, R. E., Mayle, F. E., and Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* **61,** 215-230.

Bush, M. (1991). Modern pollen-rain data from South and Central America: a test of the feasibility of fine-resolution lowland tropical palynology *The Holocene* **1,** 162-167.

Bush, M., and Rivera, R. (1998). Pollen Dispersal and Representation in a Neotropical Rain Forest. *Global Ecology and Biogeography Letters* **7,** 379-392.

Bush, M. B., De Oliveira, P. E., Colinvaux, P. A., Miller, M. C., and Moreno, J. E. (2004). Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214,** 359.

Bush, M. B., Moreno, E., De Oliveira, P. E., Asanza, E., and Colinvaux, P. A. (2001). The influence of biogeographic and ecological heterogeneity on Amazonian pollen spectra. *Journal of Tropical Ecology* **17,** 729-743.

Bush, M. B., and Riviera, R. (2001). Reproductive ecology and pollen representation among neotropical trees. *Global Ecology and Biogeography* **10,** 359-367.

Bush, M. B., Silman, M. R., and Listopad, C. M. C. S. (2007). A regional study of Holocene climate change and human occupation in Peruvian Amazonia. *Journal Of Biogeography* Special Issue 1-15.

Bush, M. B., and Weng, C. Y. (2007). Introducing a new (freeware) tool for palynology. *Journal of Biogeography* **34,** 377-380.

Clapperton, C. M. (1993). "Quaternary Geology and Geomorphology of South America." Elsevier, Amsterdam.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C. and Bush, M.B. (1996). A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* **274**, 85-88.

Colinvaux, P. A., and De Oliveira, P. E. (2000). Palaeoecology and climate of the Amazon basin during the last glacial cycle. *Journal Of Quaternary Science* **15,** 347-356.

Colinvaux, P. A., and De Oliveira, P. E. (2001). Amazon plant diversity and climate through the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166,** 51-63.

Colinvaux, P. A., De Oliveira, P. E., and Bush, M. B. (2000). Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19,** 141-169.

Colinvaux, P. A., De Oliveira, P. E., and Moreno, P. J. E. (1999). "Amazon Pollen Manual and Atlas." Harwood Academic Publishers, Amsterdam.

Condit, R., Hubbell, S. P., La Frankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B. and Ashton, P. S. (1996). Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* **84**, 549-562.

Cowling, S. A., Maslin, M. A., and Sykes, M. T. (2001). Paleovegetation Simulations of Lowland Amazonia and Implications for Neotropical Allopatry and Speciation. *Quaternary Research* **55,** 140.

Cowling, S. A., Betts, R. A., Cox, P. M., Ettwein, V. J., Jones, C. D., Maslin, M. A. and Spall, S. A. (2005). Modelling the past and future fate of the Amazonian forest. In Y Malhi, OL Phillips (Eds.), *Tropical forests and global atmospheric change.* Oxford University Press: Oxford.

Cowling, S. A., and Shin, Y. (2006). Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO_2 within a region of Amazonia. *Global Ecology and Biogeography* **15,** 553-566.

Datwyler, S. L., and Weiblen, G. D. (2004). On the origin of the fig: Phylogenetic relationships of Moraceae from *ndhF* sequences. *American Journal of Botany* **91,** 767-777.

Davis, M. B. (1963). On the theory of pollen analysis. *American Journal of Science* **261,** 897-912.

de Freitas, H. A., Pessenda, L. C. R., Aravena, R., Gouveia, S. E. M., de Souza Ribeiro, A., and Boulet, R. (2001). Late Quaternary Vegetation Dynamics in the Southern Amazon Basin Inferred from Carbon Isotopes in Soil Organic Matter. *Quaternary Research* **55,** 39.

de Oliveira-Filho, A. T. (1992). The vegetation of Brazilian 'murundus' – the island-effect on the plant community. *Journal of Tropical Ecology* **8,** 465-486.

Duivenvoorden, J. F. (1996). Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica* **28,** 142-158.

Elenga, H., de Namur, C., Vincens, A., Roux, M., and Schwartz, D. (2000). Use of plots to define pollen-vegetation relationships in densely forested ecosystems of Tropical Africa. *Review of Palaeobotany and Palynology* **112,** 79.

Fagerlind, F. (1952). The real significance of pollen diagrams. *Botanisker Notiser* **2,** 185-224.

Gentry, A. H. (1982). Patterns of neotropical plant species diversity. Evolutionary Biology **15**, 1-84.

Gentry, A. H. (1987). Tree species richness in upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* **85,** 156-159.

Gosling, W. D. (2004). Characterization of Neotropical forest and Savannah Ecosystems by their Modern Pollen Spectra. *Unpublished PhD Thesis.*

Gosling, W. D., Mayle, F. E., Tate, N. J., and Killeen, T. J. (2005). Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research* **64,** 284-297.

Haberle, S. (1997). Upper Quaternary vegetation and climate history of the Amazon Basin: Correlating marine and terrestrial pollen records. In Flood, R.D., Piper, D.J.W., Klaus, A. and Peterson, L.C., (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 155: College Station, TX.

Haberle, S.G. and Maslin, M.A. (1999). Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon Fan, ODP site 932. *Quaternary Research* **51**, 27-38.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165,** 131-137.

Haffer, J., and Prance, G. T. (2001). Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* **16,** 579-607.

Hicks, S., and Birks, H. J. B. (1996). Numerical analysis of modern and fossil pollen spectra as a tool for elucidating the nature of fine-scale human activities in boreal areas. *Vegetation History and Archaeobotany* **5,** 257-272.

Hooghiemstra, H., and Van der Hammen, T. (1998). Neogene and Quaternary development of the neotropical rainforest: the forest refugia hypothesis, and a literature overview. *Earth Science Reviews* **44,** 147-183.

Houghton, R. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T. and Chomentowski, W. H. (2000). Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* **403**, 301-304.

Huntley, B. (1996). Quaternary palaeoecology and ecology. *Quaternary Science Reviews* **15,** 591-606.

Irion, G., Bush, M.B., Nunes de Mello, J.A., Stüben, D., Neumann, T., Müller, G., Morais de, J.O. and Junk, J.W. (2006). A multiproxy palaeoecological record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **240**, 523-535.

Islebe, G. A., and Hooghiemstra, H. (1997). Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews* **16,** 589-604.

Kastner, T. P., and Goni, M. A. (2003). Constancy in the vegetation of the Amazon Basin during the Pleistocene: Evidence from the organic matter composition of Amazon deep sea fan sediments. *Geology* **31,** 291-294.

Kent, M. and Coker, P. (1994). *Vegetation Description and Analysis: A Practical Approach*. John Wiley and Sons: Chichester.

Killeen, T. J. (1998). "Vegetation and flora of Noel Kempff Mercado National Park." Conservation International, Washington, DC.

Killeen, T. J., Siles, T. M., Grimwood, T., Tieszen, L. L., Steininger, M. K., Tucker, C. J., and Panfil, S. (2002). Habitat Heterogeneity on a Forest-Savanna Ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): Implications for the Long-Term Conservation of Biodiversity in a Changing Climate *Ecological Studies* **162,** 285-312.

Lawrance, W. F., Ferreira, L. V., Rankin-de Merona, J. M. and Hutchings, R. W. (1998). Influence of plot shape on estimates of tree diversity and community composition in central Amazonia. Biotropica **30**, 662-665.

Lawrance, W. F., Albernaz, A. K. M., Fearnside, P. M., Vasconcelos, H. L., and Ferreira, L. V. (2004). Deforestation in Amazonia. *Science* **304** (5674), 1109.

Legendre, P. and Gallagher E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**(2): 271-280.

Leps, J. and Smilauer, P. (2003). *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press: Cambridge.

Maher, L. J. (1981). Statistics For Microfossil Concentration Measurements Employing Samples Spiked With Marker Grains. *Review Of Palaeobotany And Palynology* **32,** 153-191.

Marchant, R., Almeida, L., Behling, H., Berrio, J. C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., de Oliveira, A. T., Lozano-Garcia, S., Hooghiemstra, H., Ledru, M. P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., and Salgado-Labouriau, M. L. (2002). Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review Of Palaeobotany And Palynology* **121,** 1-75.

Maslin, M. A. and Burns, S. J. (2000). Reconstruction of the Amazon Basin effective moisture availability over the past 14 000 years. *Science* **290**, 2285–2287.

Maslin, M. (2005). The longevity and resilience of the Amazon rainforest. In: Y. Malhi and O. Phillips (Eds.). Tropical forests and global atmospheric change. Oxford University Press, Oxford.

Mayle, F.E., Burbridge, R.E. and Killeen, T.J. (2000). Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**, 2291-2294.

Mayle, F.E. and Beerling, D. J. (2004). Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography Palaeoclimatology Palaeoecology* **214**(1-2): 11-25.

Mayle, F.E., Beerling, D.J., Gosling, W.D. and Bush, M.B. (2004). Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society London B* **359**, 499-514.

Mayle, F. E., and Bush, M. (2005). Amazonian ecosystems and atmospheric change since the last glacial maximum. *In* "Tropical forests and global atmospheric change." (Y. Malhi, and O. Phillips, Eds.), pp. 183-190. Oxford University Press, Oxford.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., and Schloss, A. L. (1993). Global Climate-Change and Terrestrial Net Primary Production. *Nature* **363**, 234-240.

Moore, P. D., Webb, J. A., and Collinson, M. E. (1991). "Pollen Analysis." Blackwell Scientific Publications, Oxford.

Mourguiart, P. and Ledru, M-P. (2003). Last glacial maximum in an Andean cloud forest environment. *Geological Society of America*, **31**, 195-198.

Nebel, G., Kvist, L. P., Vanclay, J. K., Christensen, H., Freitas, L., and Ruiz, J. (2001). Structure and floristic composition of flood plain forests in the Peruvian Amazon I. Overstorey. *Forest Ecology and Management* **150,** 27-57.

Oksanen, J., Kindt, R., Legendre, P. and O'Hara, R.B. (2007). Vegan: Community Ecology Package version 1.8-5. http://cran.r-project.org.

Olsen, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Louks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* **51,** 933-938.

Pardoe, H. S. (2006). Surface pollen deposition on glacier forelands in southern Norway I: local patterns of representation and source area at Storbreen, Jotunheimen. *Holocene* **16,** 1149-1161.

Pennington, R. T., Prado, D. E., and Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27,** 261-273.

Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L. et al. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature* **418**, 770-774.

Phillips, O.L., Martinez, R.V. , Nunez Vargas, P., Monteagudo, A.L., Zans, M.C., Sanchez, W.G., Cruz, A.P., Timana, M., Yli-Halla, M. and Rose, S. (2003). Efficient

plot-based floristic assessment of tropical forests. Journal of Tropical Ecology **19**, 629-645.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill. D.A., Vargas, P.N., Natalino, J., Silva, N., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, E.M., Olivier, J., Palacios, W., Patino, S., Pitman, N., Quesada, C.A., Saldias, M., Lezama, A.T. and Vinceti, B. (2005). Late twentieth-century patterns and trends in Amazon tree turnover. In: Y. Malhi and O. Phillips (Eds.) *Tropical Forests and Global Atmospheric Change*. Oxford University Press, Oxford.

Phillips, O.L. and Malhi, Y. (2005). The prospects for tropical forests in the twenty-first-century atmosphere. In: Y. Malhi and O. Phillips (Eds.) *Tropical Forests and Global Atmospheric Change*. Oxford University Press, Oxford.

Prado, D. E., and Gibbs, P. E. (1993). Patterns of species distribution in the seasonally dry forests of South America. *Annals of the Missouri Botanical Gardens* **80,** 902-927.

Prance, G. T. (1979). Notes on the Vegetation of Amazonia .3. Terminology of Amazonian Forest Types Subject to Inundation. *Brittonia* **31,** 26-38.

Prance, G. T. (1982). Forest refuges: evidence from woody angiosperms. *In* "Biological diversification in the tropics." (G. T. Prance, Ed.), pp. 137-157. Columbia University Press, New York.

Prance, G. T. (1989). American Tropical Forests. *In* "Tropical Rain Forest Ecosystems. Ecosystems of the World 14B." (H. Lieth, and M. J. A. Werger, Eds.), pp. 99-132. Elsevier, Amsterdam.

Prentice, I. C. (1980). Multidimensional scaling as a research tool in Quaternary Palynology: a review of theory and methods. *Review of Palaeobotany and Palynology* **31**: 71-104.

Roa, P. R. (1980). Algunos aspectos de la evolucion sedimentologica y geomorfologica de la Llanura aluvial de desborde en el Bajo Llano. *Sociedad Venezolana de Ciencias Naturales* **35,** 31-47.

Rodgers, J. C., and Horn, S. P. (1996). Modern pollen spectra from Costa Rica. *Palaeogeography Palaeoclimatology Palaeoecology* **124,** 53-71.

Roubic, D. W., and Moreno, P. J. E. (1991). Pollen and Spores of Barro Colorado Island. *Monographs in Systematic Botany* **36**.

Salgado-Labouriau, M. L. (1997). Late-Quaternary paleoclimate in the savannas of South America. *Journal of Quaternary Science* **12,** 371-379.

Seltzer, G. O., Rodbell, D. T., Burns, S. (2000). Isotopic evidence for late quaternary climatic change in tropical South America. *Geology* **28**, 35-38.

Servant, M., Fontes, J.-C., Rieu, M. and Salie`ge, J.-F. (1981). Phases climatiques arides holocènes dans le sud-ouest de l'Amazonie (Bolivie). *C. R. Acad. Sci. Paris* **292**, Sèrie II, 1295–1297.

Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubies, F., Cordeiro, R. C. and Suguio, K. (2001). Variations of the Amazon rainforest environment: a sedimentological record covering 30 000 years. *Palaeogeography Palaeoclimatology Palaeoecology*, 168, 221-235.

Sioli, H. (1968). Hydrochemistry and geology in the Brazilian Amazon region. *Amazonica* **5,** 51-76.

Sneath, P. H. A. and Snokal, R. R. 1973. *Numerical Taxonomy*. Freeman: San Fransisco.

Soil Survey Staff, Natural resources conservation service, United States Department of Agriculture. Soil Series Classification Database. Available URL:

"http://soils.usda.gov/soils/technical/classification/scfile/index.html" [Accessed 2 February 2008].

Stockmarr, J. (1971). Tablets with spores used in absolute pollen analysis. *Pollen Spores* **13,** 615-621.

ter Braak, C. J. F. (1986). Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J. F., Prevost, M. F., Spichiger, R., Castellanos, H., von Hildebrand, P., and Vasquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443,** 444-447.

Thompson, L.G., E. Mosley-Thompson, M. E. Davis, P-N. Lin, K. A. Henderson, J. Cole-Dai, J. F. Bolzan and K-b. Liu. (1995). Late Glacial Stage and Holocene tropical ice core records from Huascarán, Peru. *Science* **269**, 46-50.

Thompson, L.G., M.E. Davis, E. M.Thompson, T. A.Sowers, K. A. Henderson, V. S. Zagorodnov, P. N. Lin, V. N. Mikhalenko, R. K. Campen, J. F.Bolzan, J.Cole-Dai and Francou, B. (1998). A 25,000 year tropical climate history from Bolivian ice cores. *Science* **282**, 1858-1864.

Tian, H. Q., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich, J. V. K., Moore, B. and Vorosmarty, C. J. (1998). Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**(6712), 664-667.

Valdes, P.J. (2000). South American palaeoclimate model simulations: how reliable are the models? *Journal of Quaternary Science* **15**, 357-368.

Vincens, A., Dubois, M. A., Guillet, B., Achoundong, G., Buchet, G., Beyala, V. K. K., de Namur, C., and Riera, B. (2000). Pollen-rain-vegetation relationships along a forest-savanna transect in southeastern Cameroon. *Review Of Palaeobotany And Palynology* **110,** 191-208.

Van der Hammen, T. and Absy, M. L. (1994). Amazonia During the Last Glacial. *Palaeogeography Palaeoclimatology Palaeoecology* **109**(2-4): 247-261.

Vascular Tropicos Nomenclatural Database (2007). Published on the internet http://mobot.mobot.org/W3T/Search/vast.html [accessed 8 January 2007].

Waller, M. P., Binney, H. A., Bunting, M. J., and Armitage, R. A. (2005). The interpretation of fen carr pollen diagrams: pollen–vegetation relationships within the fen carr. *Review of Palaeobotany and Palynology* **133,** 179-202.

Weng, C., Bush, M. B. and Athens, J. S. (2002). Holocene climate change and hydrarch succession in lowland Amazonian Ecuador. *Review of Palaeobotany and Palynology*, **120**, 73-90.

Weng, C. Y., Bush, M. B., and Silman, M. R. (2004). An analysis of modern pollen rain on an elevational gradient in southern Peru. *Journal of Tropical Ecology* **20,** 113-124.

Wittmann, F., Schongart, J., Montero, J. C., Motzer, T., Junk, W. J., Piedade, M. T. F., Queiroz, H. L., and Worbes, M. (2006). Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* 33, 1334-1347.

Chapter 2 Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology

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2.1 Abstract

The Moraceae family is one of the most abundant and ecologically important families in Neotropical rainforests and is very well represented in Amazonian fossil pollen records. However, difficulty in differentiating palynologically between the genera within this family, or between the Moraceae and Urticaceae families, has limited the amount of palaeoecological information that can be extracted from these records. The aim of this paper is to analyse the morphological properties of pollen from Amazonian species of Moraceae in order to determine whether the pollen taxonomy of this family can be improved. Descriptive and morphometric methods are used to identify and differentiate key pollen types of the Moraceae (mulberry) and Urticaceae (nettle) families which are represented in Amazonian rainforest communities of Noel Kempff Mercado National Park (NKMNP), Northeast Bolivia. We demonstrate that *Helicostylis*, *Brosimum*, *Pseudolmedia*, *Sorocea* and *Pourouma* pollen can be identified in tropical pollen assemblages. We present digital images of, and a taxonomic key to, the Moraceae pollen types of NKMNP. Indicator species,

Maquira coriacea (riparian evergreen forest) and *Brosimum gaudichaudii* (open woodland and upland savanna communities), also exhibit unique pollen morphologies. The ability to recognise these ecologically important taxa in pollen records provides the potential for much more detailed and reliable Neotropical palaeovegetation reconstructions than have hitherto been possible. In particular, this improved taxonomic resolution holds promise for resolving long-standing controversies over the interpretation of key Amazonian Quaternary pollen records.

Key words: Moraceae, pollen, Quaternary, Bolivia, Amazon Basin, rainforest, morphology, riparian forest.

2.2 Introduction

There is considerable controversy regarding the interpretation of Amazonian fossil pollen records (Colinvaux and De Oliveira, 2000; Pennington et al., 2000; Bush, 2002; Bush et al., 2004; Mayle et al., 2004; Anhuf et al., 2006), which hampers progress in our understanding of Late Quaternary vegetation dynamics, the testing of climate and 'earth-system' models (Valdez, 2000; Cowling et al. 2005) and in obtaining improved estimates of past carbon storage (Behling, 2002; Mayle and Beerling, 2004; Beerling and Mayle, 2006). Much of this controversy arises from the sparse distribution of fossil pollen sites within the Amazon Basin and the extent to which they are representative of Amazonia as a whole. More problematic, however, is our inability to identify many Amazonian pollen types to species, or even genus level, resulting in poor taxonomic resolution in many fossil pollen records. Pennington et al. (2000) point out that, when operating at such a low taxonomic

resolution, up to 80% of fossil pollen types attributed to 'tropical rain forest' taxa, equally characterise 'seasonally dry forest' taxa (e.g. Pleistocene pollen assemblages of Lake Pata in central Amazonia, Colinvaux et al., 1996). This sizeable overlap may be overcome with the increasing availability of pollen rain data that establish pollen signatures for tropical forest communities based upon differences in the abundance of their constituent taxa (e.g. Bush et al., 2004; Weng et al., 2004; Gosling et al., 2005). Similarly, improving the taxonomic resolution at which Amazonian pollen can be identified, should allow these communities to be much more readily differentiated by the presence or absence of ecosystem-specific indicator taxa.

The mulberry family (Moraceae) comprises ca. 37 genera and over 1100 species worldwide and is one of the most abundant and ecologically important families growing in tropical rainforests of Central and South America (Datwyler and Weiblen, 2004). This family forms part of the Rosidae and is closely allied to the Urticalean rosids that include Cannabaceae, Celtidaceae, Urticaceae, Cecropiaceae and Ulmaceae. In general, Moraceae plants are monoecious or dioecious trees and shrubs, and are adapted to a wide range of moist tropical evergreen forest habitats including well-drained *terra firme* forest, liana dominated forest, as well as seasonally inundated and riparian forests (Killeen, 1998). They exhibit high Family Importance Values (FIV; a composite index of relative density, diversity and dominance) across the Amazon Basin and are well-represented in drought-adapted liana forests (FIV = 19; Salvias Project, 2007) as well as *terra firme* forests (FIV = 32) in northeast Bolivia. Moraceae species are at their most abundant and diverse in *várzea* (seasonally flooded) forests of tropical lowland Amazonia, exemplified by

high importance values in Ecuador (FIV = 44; Baslev et al., 1987), Peru (FIV = 51; Nebel et al., 2001a) and northeast Bolivia (FIV = 80; Salvias Project, 2007).

Constituent species are highly specialised and adapted to a diverse range of habitats. The várzea tree *Maquira coriacea* (Karsten) C. C. Berg, for example, is restricted to, and regularly dominates, flood plain forests of the Amazon, Orinoco and upper Rio Paraguay Basins (Nebel et al., 2001b). In contrast, *Helicostylis tomentosa* (Poepp. & Endl) J. F. Macbr flourishes in well-drained (*terra firme*) tall evergreen rainforests and liana forests (Killeen, 1998). The shrub *Brosimum gaudichaudii* Trecul prefers rather more arid environments and grows in both open woodland and *cerrado* (well-drained savanna) communities along the southwestern margin of the Amazon Basin (De Oliveira-Filho, 1992; Marchant et al., 2002).

Such diversity and importance of species within the Moraceae family is, however, not well captured in Amazonian fossil pollen records. Moraceae pollen is generally only identified to the family taxonomic level and has hitherto been grouped together with the nettle family (Urticaceae) because of morphological similarity between grains (e.g. Colinvaux et al., 1996; Haberle and Maslin, 1999; Behling and Hooghiemstra, 2000; Mayle et al., 2000;). Pollination strategies of constituent genera are mostly anemophilous and therefore regularly over-represented in pollen spectra (Gosling et al., 2005). *Ficus* and *Castilla* are exceptions, exhibiting obligate mutualism with pollinating fig-wasps and thrips, respectively (Bush and Riviera, 2001; Sakai, 2001; Datwyler and Weiblen, 2004). These two genera are cleistogamous and therefore heavily under-represented in pollen assemblages. Indeed, Bush and Riviera (2001) have calculated that, in the pollen flora of Barro

Colorado Island, *Ficus* has a very low R-rel value (% mean pollen influx / % basal area) of 0.03.

Moraceae/Urticaceae type pollen regularly accounts for 10-60% of total pollen counts and is considered to indicate the presence of closed-canopy lowland tropical rain forest communities when pollen abundance is > 30% (Mayle et al., 2004; Gosling et al., 2005). Notwithstanding a few attempts to separate *Brosimum* (Irion et al., 2006) and *Ficus* (Bush and Colinvaux 1988; Liu and Colinvaux, 1988) from the Moraceae/Urticaceae category in pollen assemblages, little work has been done to identify constituent pollen types to a higher taxonomic resolution.

Here, we present the first detailed analysis of the morphological properties of Moraceae and Urticaceae pollen grains of the Amazon Basin. Using descriptive and morphometric methods we attempt to differentiate between pollen of the constituent genera of the Moraceae and Urticaceae families represented within different kinds of rainforest community in Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. In particular, we aim to provide a pollen-taxonomic key that can be used by Neotropical palynologists to identify Moraceae and Urticaceae genera and species.

2.3 Study Area

Taxa were selected for palynological study from detailed floristic inventories of plant communities within Noel Kempff Mercado National Park (NKMNP), a 15,230 km^2 biological reserve in northeast Bolivia that occupies part of the Madeira-Tapajós ecoregion (Olsen et al., 2001; Fig. 2.3-1). The park is situated on an ecotone spanning 22 pristine plant communities, from moist evergreen rainforest in the north, to *cerrado* (well-drained savanna) in the east, and semi-deciduous dry-forest

communities in the south, and provides a physical setting that supports considerable ecosystem diversity (Killeen et al., 2003). Two black-water rivers, the Rio Iténez and Rio Paraguá define the eastern and western boundaries of NKMNP, respectively. Precambrian rocks of the Huanchaca Plateau (600-900 m a.s.l.) characterise the eastern half of the park, and Tertiary alluvial deposits of the lowland peneplain (200-250 m a.s.l.), the western half.

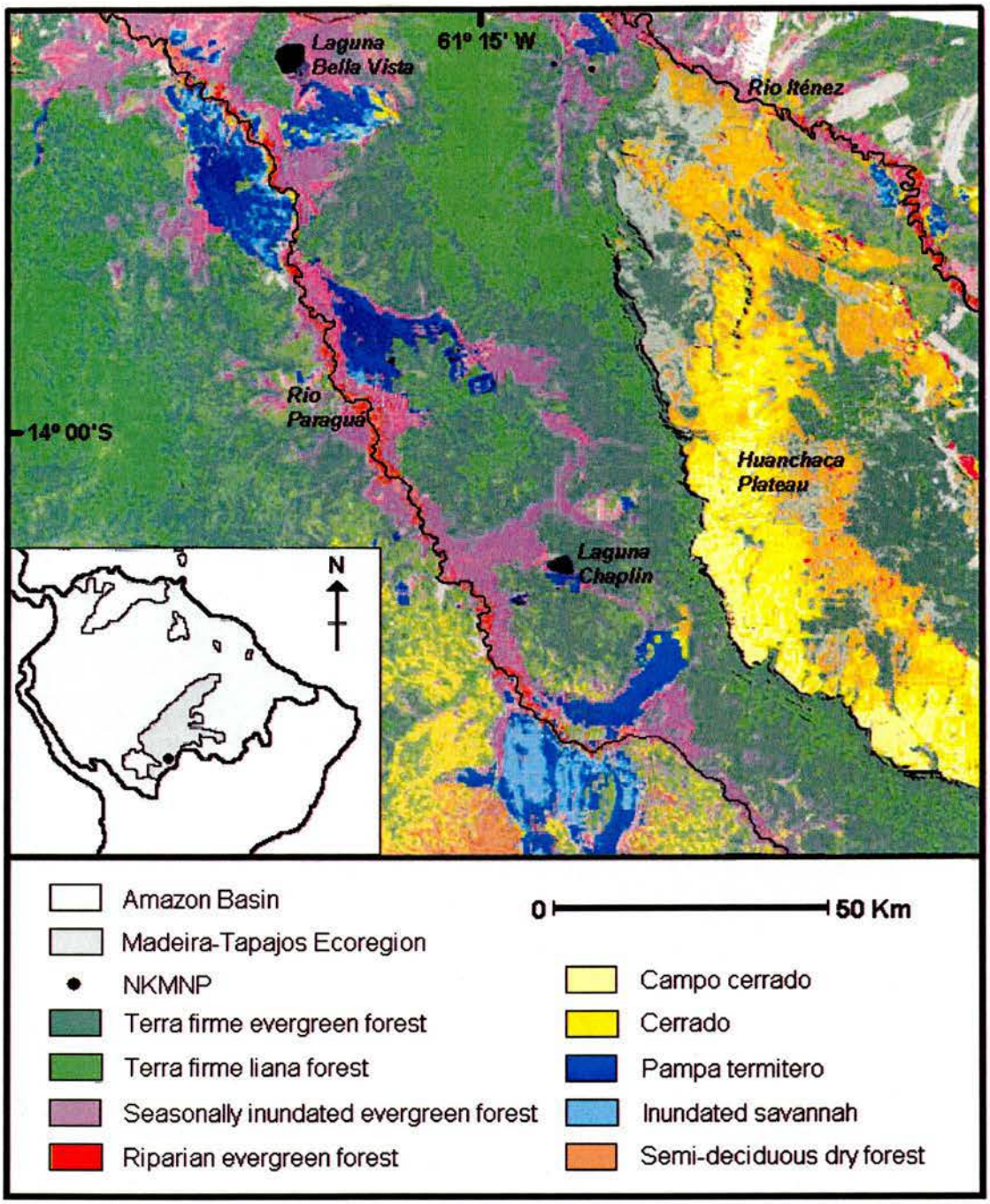

Fig. 2.3-1: Location map (inset) and distribution of plant communities within Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. Modified from Killeen and Schulenberg (1998).

The vegetation of the Huanchaca Plateau consists mainly of *cerrado* savanna communities, which are well-adapted to dystrophic soils overlying the basement rocks of the Precambrian Shield. Here, moist evergreen gallery forest is confined to valleys or depressions with sufficiently thick soils (Killeen, 1998). In contrast, a

variety of evergreen rainforest communities dominate the neighbouring alluvial plains, which are characterised by moist deep soils. High evergreen rainforest and liana forest grow on well-drained (*terra firme*) soils, while riparian and seasonally-flooded rainforests, as well as seasonally-flooded savannas, are associated with the seasonal flooding regime of the Rio Paraguá. Such high ecosystem diversity (*beta* diversity) within the park is responsible for a diverse range of Moraceae species (Killeen, 1998), many of which are restricted to specific kinds of rainforest. Fossil pollen analyses of sediments from the two large lakes in NKMNP, Laguna Chaplin (14° 28' S, 61° 04' W) and Laguna Bella Vista (13° 37' S, 61° 33' W), have revealed changes in vegetation, fire dynamics, and climate, over the last 50,000 years (Burbridge et al., 2004; Mayle et al., 2000).

2.4 Materials and methods

2.4.1 *Selection of species for palynological study*

Detailed floristic inventories were obtained from one hectare (500 × 20 m) study plots from each of the 22 plant communities within NKMNP between 1993 and 2000 by Killeen (1998) and are readily available from the Salvias Project database (2007). Every woody plant ≥ 10 cm d.b.h. (diameter at breast height) has been measured and all tagged specimens are stored at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia. Identification was made by comparison with specimens held in the collection in Santa Cruz and at the Missouri Botanical Gardens (Killeen and Schulenberg, 1998). Standardized nomenclature presented here is in accordance with publications cited in the International Plant Names Index (2007), a combination of Index Kewensis, the Gray Card Index and the

Australian Plant Names Index. Pollen of key species of each genus of Moraceae and Urticaceae recorded in these vegetation study plots was analysed (Table 2.5-1).

Of all the ecosystems in the study area, the following four rainforest communities exhibited the greatest abundance and diversity of Moraceae species: *terra firme* tall evergreen forest, evergreen liana forest, seasonally-inundated evergreen forest and riparian evergreen forest. Species represented in other plant communities included *Brosimum alicastrum* (gallery forest lining savanna rivers on the Huanchaca plateau; Killeen, 1998), *Brosimum gaudichaudii* (open woodland, *campo cerrado* (open *terra firme* savanna), and seasonally-inundated savanna communities) and two *Pourouma* species, *P. guianensis* and *P. minor* (gallery forest and semi-deciduous dry forest, respectively) that have recently been re-classified as Cecropiaceae (IPNI, 2007) but share similar pollen-morphological characteristics with Moraceae/Urticaceae.

The Urticaceae species were not represented in any rainforest or *cerrado* plots within NKMNP, with the sole exception of *Urera*, which is found in liana forests with a negligible importance value (IVI) of 0.35. Given that Urticaceae is an herbaceous family, it is possible that plants below 10 cm d.b.h. may have been present in the plots and consequently not listed in the floral inventories. However, this shade-intolerant herbaceous family is unlikely to be found within the understorey of closed-canopy rainforest communities where it would be out-competed by tree species better adapted to light-restricting environments. Indeed, *Urera caracasana* is a fast-growing pioneer species which flourishes only when openings occur as a result, for example, of tree fall (Orozco-Segovia et al. 1987). Furthermore, the understorey of both riparian and seasonally inundated communities is sparsely

populated due to flooding throughout much of the year (Killeen, 1998) and woody species < 10 cm d.b.h. are poorly represented. Of the Urticaceae, *Urera caracasana* and *Poulzolzia poeppigiana* were selected for morphometric analyses.

2.4.2 *Pollen processing and microscopic analysis*

Mature male flowers were collected from the herbaria of the 'Noel Kempff Mercado' Natural History Museum in Santa Cruz, Bolivia and the Royal Botanic Garden Edinburgh, Scotland. Sufficient pollen for processing was collected from all taxa except *Brosimum acutifolium*. Samples were soaked in 10% NaOH for a few hours (to soften the material and extract humic acids), sieved through a 250μm sieve, and prepared for light microscopy following the standard acetolysis method of Faegri and Iverson (1989). Residues were suspended in silicone oil for morphometric analysis. For each species, measurements were made on mature pollen grains (n = 30) at ×1000 magnification under an oil immersion Olympus BX 50 light microscope. Digital images were taken with a Canon Eos 350D digital camera. Morphological descriptions included size, aperture number, sculpturing, polarity, symmetry and the presence/absence of annulus and operculum. The shape class of individual grains was obtained by measurement of the following geometric parameters: The lengths of the polar axis (P) and longest equatorial diameter (E) were measured on all grains with a precision of 0.5μm. The length of the shortest equatorial diameter, depth (D), was measured to distinguish between ellipsoid diporate grains (Fig 2.4-1). Shape classes were quantified using P/E and P/D ratios, respectively, and described according to Erdtman (1943). The non-parametric Mann Whitney U-test was used to

test for significance between the measured parameters. Terminology follows that of Punt et al. (2007).

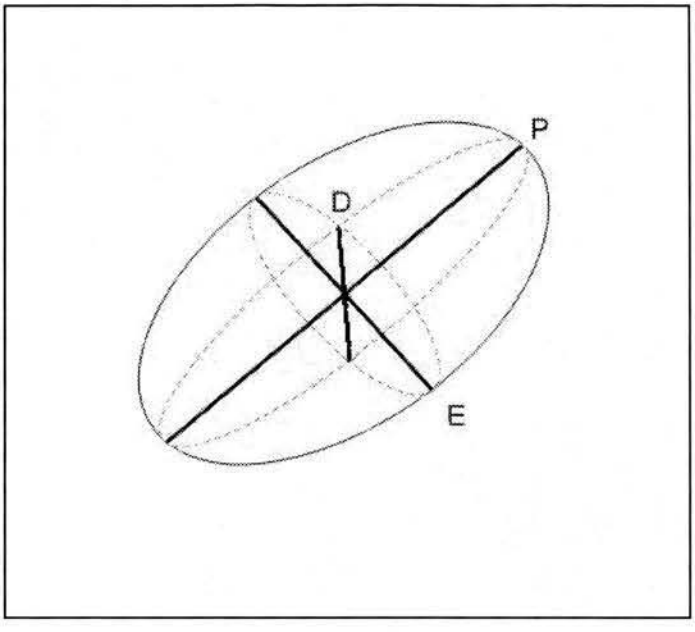

Fig. 2.4-1: Schematic diagram illustrating the three parameters measured to distinguish the shape class of ellipsoid diporate pollen grains. P = Polar axis length, E = length of the longest equatorial diameter, D = length of the shortest equatorial diameter.

2.5 Results

Table 2.5-1 provides a summary of the quantitative parameters measured for all pollen specimens alongside habitat requirements for parent species. Digital images of studied pollen grains are presented in Fig. 2.5-1 and a taxonomic key to the genera and species of Moraceae and Urticaceae pollen types of NKMNP is given in Appendix 1 alongside concise pollen descriptions. All grains are isopolar monads with tectate exines; pores are always circular and some grains exhibit a slight protrusion or thickening of the exine around the pores (annulus *sensu* Punt et al., 2007). Sculpturing of the sexine is usually psilate or scabrate. The shape class (P/E)

varies between oblate and sub-prolate, with grains of some genera, such as *Brosimum* and *Sorocea*, exhibiting spheroidal characteristics. The shape class (P/D) for diporate grains varies from prolate (e.g. *Pourouma*) to spheroidal (e.g. *Brosimum lactescens*, *B. alicastrum*). All 3-4 and 5 porate grains are angulaperturate in polar view. Specific morphological characteristics are discussed below.

Table 2.5-1: Results of descriptive and morphometric analyses of pollen grains examined including habitat details for parent taxa

Species	Specimen N°	Family	Habitat	n	Polarity	# apertures	Mean E (µm)	Mean P (µm)	Mean D (µm)	P/E	Shape Class	P/D	Other distinctive features	Annulus	Pore size (µm)	Sculpturing	Operculum
Brosimum alicastrum Sw.	JW10038	Moraceae	TEFab	30	isopolar	2	18.17	18.10	16.67	1.00	spheroidal	1.09		Yes	3	scabrate	Yes
Brosimum guianense (Aubl.) Huber	JR6295	Moraceae	RFa, IRFa, TEFb	30	isopolar	2	15.50	15.53	12.03	1.00	spheroidal	1.29		Yes	1.5-2	scabrate	Yes
Brosimum lactescens (S. Moore) C.C. Berg	AJ1095	Moraceae	SIFb, IRFa, TEFa	30	isopolar	2	18.37	18.03	16.40	0.98	spheroidal	1.10		Yes	3	scabrate	Yes
Brosimum lactescens (S. Moore) C.C. Berg	JR 6336	Moraceae	SIFb, IRFa, TEFa	30	isopolar	2	18.07	17.93	16.23	0.99	spheroidal	1.11		Yes	3	scabrate	Yes
Brosimum gaudichaudii Trecul	KF4074	Moraceae	CEab, PTa,	30	isopolar	2	12.37	14.73	10.80	1.19	subprolate	1.37		Yes	1.5-2	psilate	No
Brosimum gaudichaudii Trecul	TK2138	Moraceae	CEab, PTa,	30	isopolar	2	11.93	14.63	10.87	1.23	subprolate	1.35		Yes	1.5-2	psilate	No
Pseudolmedia laevigata Trecul	G1913	Moraceae	SIFa, RFa	30	isopolar	3-4	16.13	13.53	*	0.84	suboblate	*	angulaperturate	No	2	psilate	No
Pseudolmedia laevis (Ruiz & Pavon) J. F. Macbr.	DN9312	Moraceae	SIFa, TEFa, LFa	30	isopolar	3-4	18.87	17.40	*	0.92	spheroidal	*	angulaperturate	No	2-3	psilate	No
Pseudolmedia macrophylla Trecul	EM898	Moraceae	TEFa	30	isopolar	3-4	19.93	18.27	*	0.92	spheroidal	*	angulaperturate	No	2	psilate	No
Maquira coriacea (Karsten) C.C. Berg	SB19657	Moraceae	RFac, IRFac	30	isopolar	3-4-5	18.67	15.67	*	0.84	suboblate	*	angulaperturate	No	2	scabrate	No
Helicostylis scabra (J.F. Macbr.) C.C. Berg	WP1210	Moraceae	TEFa, LFa	30	isopolar	2-3	11.87	9.23	*	0.78	suboblate	*	angulaperturate	No	1.5	scabrate	No
Helicostylis tomentosa (Poepp. & Endl.) J.F. Macbr.	MT1190	Moraceae	TEFa, LFa	30	isopolar	2-3	12.47	9.50	*	0.76	suboblate	*	angulaperturate	No	1.5	scabrate	No
Helicostylis tomentosa (Poepp. & Endl.) J.F. Macbr.	R7591	Moraceae	TEFa, LFa	30	isopolar	2-3	12.10	9.53	*	0.79	suboblate	*	angulaperturate	No	1.5	scabrate	No
*Ficus citrifolia*Mill.	A757	Moraceae	GFa, SDFa	30	isopolar	2	12.20	7.93	*	0.65	oblate	*		No	1-1.5	psilate	No
Ficus pertusa L.F.	TK6855	Moraceae	SIFb, IRFa, TEFa	30	isopolar	2	9.73	6.07	*	0.63	oblate	*		No	1-1.5	psilate	No
Ficus paraensis (Miq.) Miq.	J3109	Moraceae	TEFa	30	isopolar	2	14.33	9.07	*	0.64	oblate	*		No	1-1.5	psilate	No
Pourouma guianensis Aubl. subsp. *guianensis*	IGV2818	Cecropiaceae	TEFab, LFa	30	isopolar	2	13.50	14.07	10.53	1.04	spheroidal	1.34		Yes	1.5	coarsely scabrate	Yes
Pourouma minor Benoist	TK3899	Cecropiaceae	GFa, TEFb	30	isopolar	2	12.73	15.13	10.50	1.19	subprolate	1.44		Yes	1.5	coarsely scabrate	Yes
Sorocea guilleminiana Gaudich.	RF13719	Moraceae	TEFa, LFa,SIFa, SDFa	30	isopolar	2	14.50	14.70	12.67	1.05	spheroidal	1.16		No	2	coarsely scabrate	Yes
Sorocea guilleminiana Gaudich.	TK1120	Moraceae	TEFa, LFa, SIFa, SDFa	30	isopolar	2	15.00	14.87	12.40	0.99	spheroidal	1.20		No	2	coarsely scabrate	Yes
Sorocea hirtella Mildbr.	G554	Moraceae	RVa	30	isopolar	2	12.63	12.40	11.27	0.98	spheroidal	1.10		No	2	scabrate	Yes
Maclura tinctoria Steud.	G75565	Moraceae	TEFab, LFa	30	isopolar	2-3	12.27	12.17	10.53	0.99	spheroidal	1.16		No	2	scabrate	Yes
Urera caracasana (Jacq.) Gaudich. ex Griseb.	TK5928	Urticaceae	LFa, TFGd	30	isopolar	3	12.43	10.67	12.43	0.86	suboblate	*		Yes	1-1.5	psilate	Yes
Pouzolzia poeppigiana (Wedd.) Killip	MC14	Urticaceae	TFGa	30	isopolar	3	12.80	10.80	12.80	0.85	suboblate	*		Yes	1-1.5	psilate	No

Pollen-morphological terminology follows Punt et al. (2007): E, equatorial diameter; P, polar diameter; D, depth (third focal plane of ellipsoid pollen grains). Habitats: TEF, terra firme evergreen forest; RF, riparian evergreen forest; IRF, inundated riparian evergreen forest; SIF, seasonally-inundated evergreen forest; CE, cerrado (upland savanna); PT, pampa termitero (seasonally-flooded savanna); LF, terra firme liana forest; GF, gallery forest; SDF, semi-deciduous dry forest; RV, riparian vegetation; TFG, tree fall gaps. [a]Killeen and Schulenberg (1998); [b]Marchant et al. (2002); [c]Nebel et al. (2001b); [d]Orozco-Segovia et al. (1987).

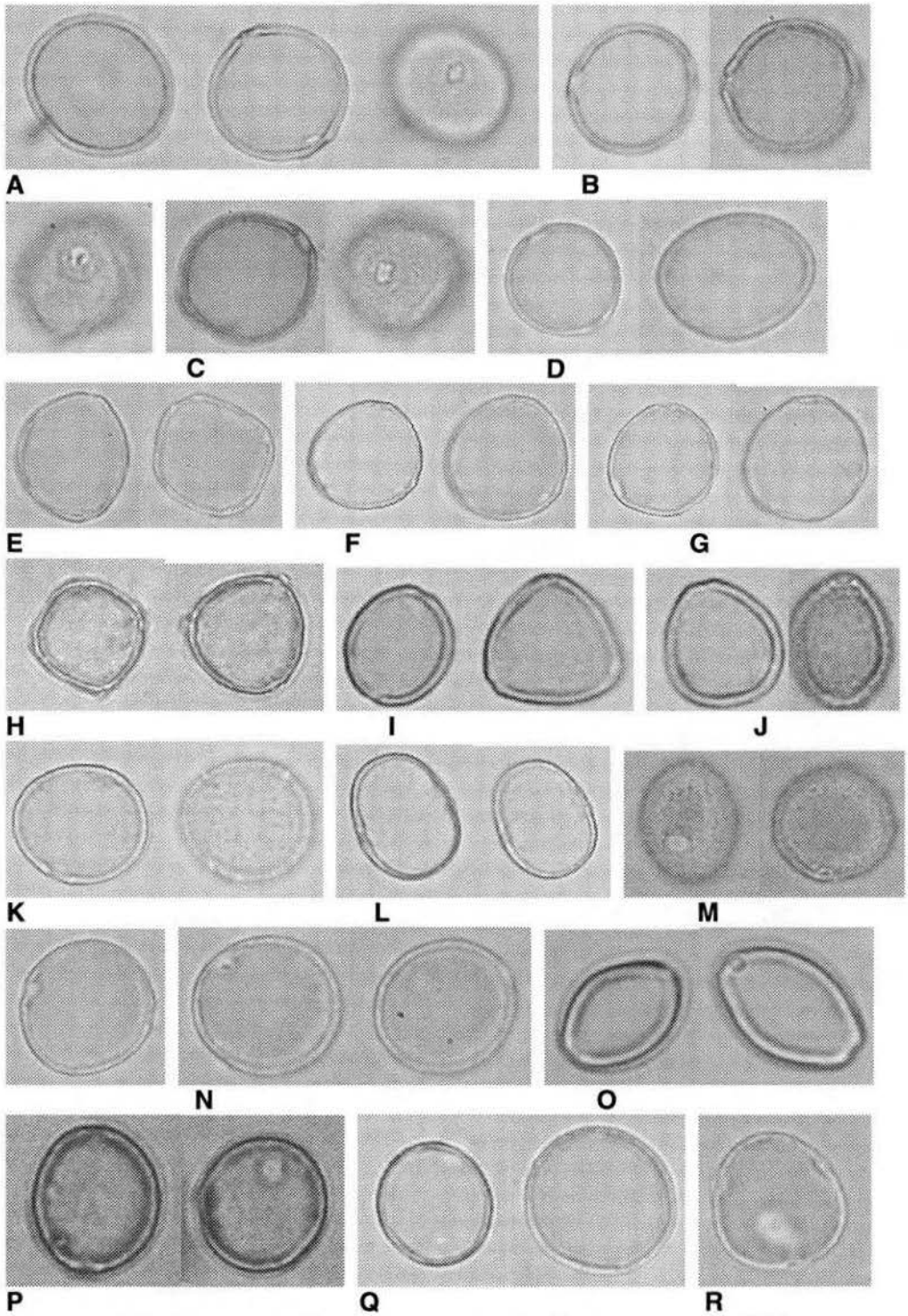

Fig. 2.5-1: Light micrographs of Moraceae/Urticaceae pollen found in NKMNP (× 1000 magnification), A: *Brosimum alicastrum*, B: *B. guianense*, C: *B. lactescens*, D: *B. gaudichaudii*, E: *Pseudolmedia laevigata*, F: *P. laevis*, G: *P. macrophylla*, H: *Maquira coriacea* I: *Helicostylis scabra*, J: *H. tomentosa*, K: *Pourouma guianensis*, L: *P. minor*, M: *Sorocea guilleminiana*, N: *S. hirtella*, O:

Ficus citrifolia P: *Maclura tinctoria*, Q: *Urera caracasana*, R: *Pouzolzia poeppiggiana*. N.B. Grains not to scale.

2.5.1 *Pollen-morphological characteristics*

2.5.1.1 Size

In general, pollen grains are small, with the mean length of the polar axis (P) varying between 6 ± 0.5 µm for *Ficus pertusa* and 18.5 ± 2 µm for *Pseudolmedia macrophylla*, and the mean equatorial diameter (E) varying between 9.5 ± 0.5 µm and 20 ± 1.5 µm for the same species, respectively (Table 2.5-1). Most grains can clearly be allocated to two distinct size classes according to their equatorial diameter, with the exception of *Pseudolmedia laevigata*, *B. guianense*, *Sorocea guilleminiana* and *Ficus paraensis,* which fall along a gradient between these classes (Fig. 2.5-2 (a)). The larger size class, with a combined mean value of 18 ± 2 µm, includes *Pseudolmedia laevis, P. macrophylla*, *Maquira coriacea*, and *Brosimum*, except for *B. gaudichaudii*. The smaller size class consists of *B. gaudichaudii, Helicostylis*, *Pourouma*, *Sorocea*, *Ficus*, *Maclura tinctoria* and both Urticaceae species, *Urera caracasana* and *Pouzolzia poeppigiana*, which have a combined mean value of 12.5 ± 1.5 µm. Differences in the mean length of the polar axes of grains show a similar trend, although the boundaries between size classes are less clear (Fig. 2.5-2 (b)). Grains with the shortest mean length of the polar axis are *Ficus* and *Helicostylis* and both Urticaceae species. *Helicostylis* and *Ficus* have mean polar axis lengths of 9.5 ± 1 and 7.5 ± 1.5 µm, respectively, significantly smaller ($p < 0.01$; Mann-Whitney U-test) than the Urticaceae species, *Urera caracasana* and *Pouzolzia poeppigiana*, which have a combined mean polar axis length of 10.5 ± 1 µm.

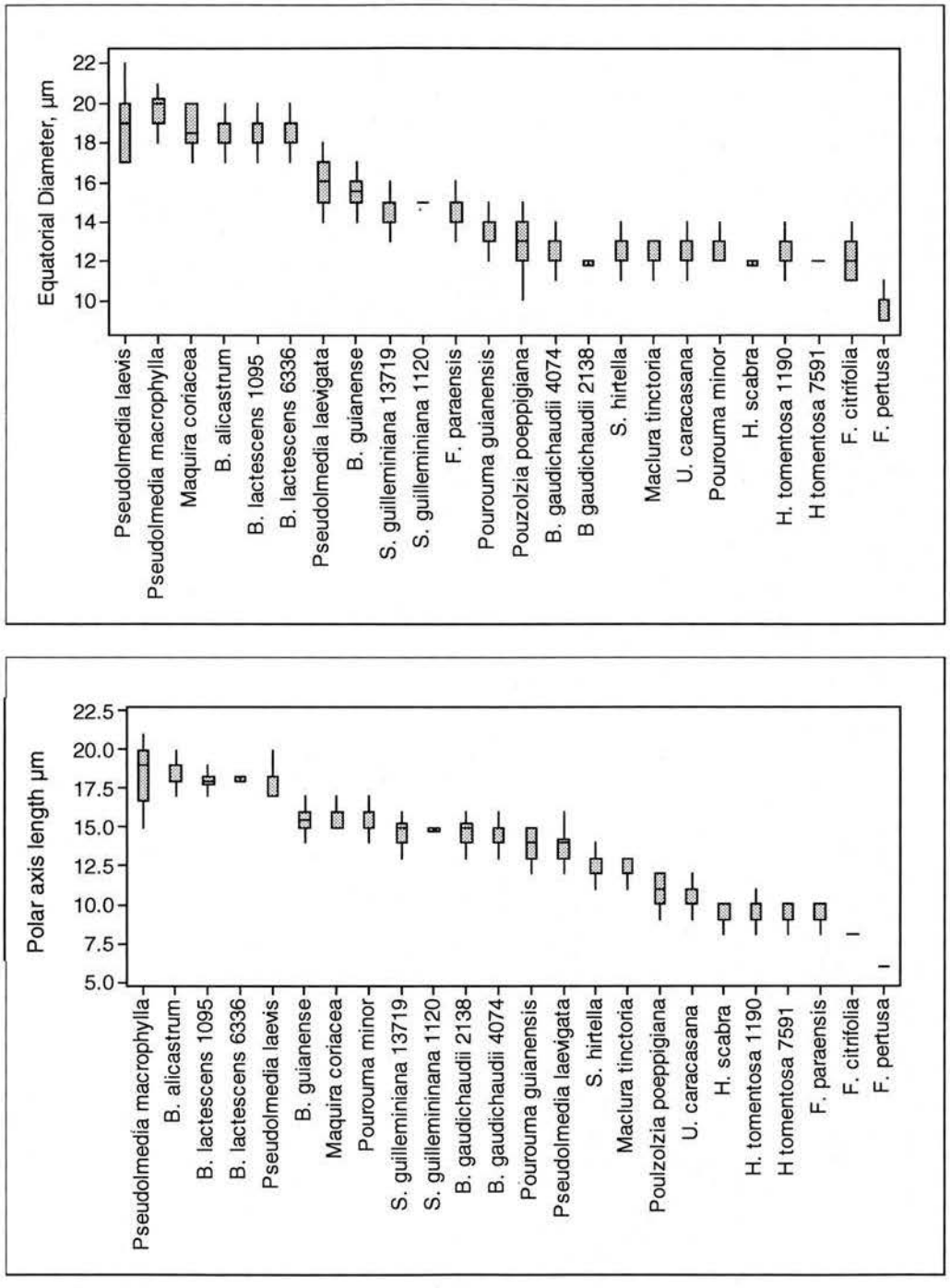

Fig. 2.5-2: Box plots of (a) equatorial diameter (E), and (b) polar axis length (P) of the Moraceae and Urticaceae pollen within NKMNP. Stems represent the range of the data; the boxes show the interquartile range.

2.5.1.2 Apertures

The number of pores allows the subdivision of key pollen types and, when allied with other morphological features, is of great diagnostic value (Appendix 1). *Brosimum*, *Pourouma*, *Sorocea* and *Ficus* are diporate and reveal no variability in pore numbers (Table 2.5-1). *Helicostylis* and *Maclura tinctoria* are 2-3 porate (Figs. 2.5-1 (I – J); 2.5-1(P)), *Pseudolmedia* 3-4 porate (Fig. 2.5-1 (E – G)) and *Maquira coriacea* 3-4-5 porate (Fig. 2.5-1 (H)). Both pollen types of the Urticaceae family, *Urera caracasana* and *Pouzolzia poeppigiana*, have three pores and display no variability in their number (Fig. 2.5-1 (Q – R)). With the exception of *B. gaudichaudii*, *Brosimum* has the largest pores with a mean diameter of 3μm (Fig. 2.5-1 (A – C)). Most other genera have a mean pore diameter ranging from 1to 2 μm, and *Urera caracasana*, *Poulzolzia poeppigiana* and *Ficus* exhibit the smallest mean pore diameter of 1-1.5μm. *Brosimum*, *Pourouma*, and both Urticaceae specimens reveal a distinct thickening (annulus) around the pores, in particular *B. lactescens*, *B. alicastrum* and *B. guianensis* (Fig. 2.5-1 (A – C)). In contrast, the genera *Pseudolmedia*, *Helicostylis*, *Sorocea*, *Ficus* and species *Maclura tinctoria* and *Maquira coriacea* do not. Opercula are present in *Sorocea*, *Pourouma*, *Maclura tinctoria*, *Urera caracasana*, and *Brosimum* (except for *B. gaudichaudii*).

2.5.1.3 Shape

Shape classes according to both the P/E and P/D ratios vary significantly between the constituent pollen types of the Moraceae and Urticaceae families (Fig. 2.5-3 (a); Appendix 1). Grains with a spheroidal shape class (P/E = 0.88 – 1.14) include *Brosimum alicastrum, B. lactescens, B. guianense, Pseudolmedia laevis, P. macrophylla, Pourouma guianensis*, *Maclura tinctoria* and *Sorocea.* Only *Pourouma*

minor and *B. gaudichaudii* have a subprolate shape class (P/E = 1.14 -1.33) and *Pseudolmedia laevigata*, *Maquira coriacea*, *Helicostylis* and the Urticaceae are suboblate (P/E = 0.75 – 0.88). *Ficus* is the only genus which has an oblate shape class (P/E = 0.5 – 0.75). Tri- and stephano- porate grains, including *Pseudolmedia*, *Helicostylis*, and *Maquira coriacea* are angulaperturate (*sensu* Punt et al. 2007; with the apertures situated at the angles of the outline in polar view; Fig. 2.5-1 (E - J)), with the exception of *Maclura tinctoria* and both Urticaceae species.

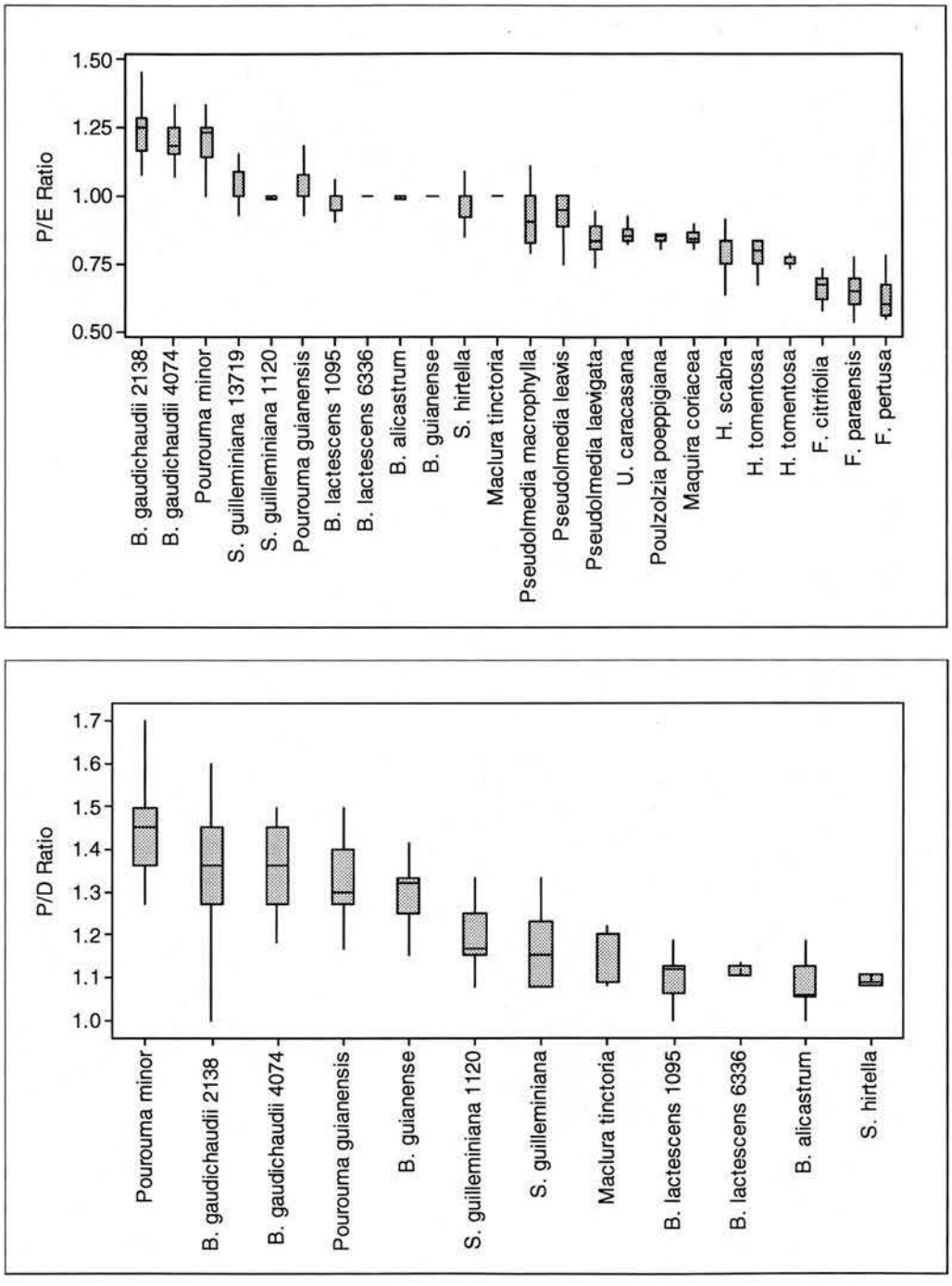

Fig. 2.5-3: Box plots of (a) P/E ratio, and (b) P/D ratio of the Moraceae and Urticaceae pollen within NKMNP. Stems represent the range of the data; the boxes show the interquartile range.

Diporate ellipsoid grains can be classified into different classes according to their P/D ratio (Fig. 2.5-3 (b); Appendix 1). *B. alicastrum*, *B. lactescens*, and *Sorocea hirtella* are spheroidal (P/D = 0.88 - 1.14), *B guianense, S. guilleminiana* and *Maclura tinctoria* are subprolate (P/D = 1.14 – 1.33), and *B. gaudichaudii* and *Pourouma* are prolate (P/D = 1.33 – 2.00). Despite being within the same shape class as *S. guilleminiana* (P/D = 1.18) and *Maclura tinctoria* (P/D = 1.16), *B. guianense* has a significantly different P/D ratio (1.29; $p < 0.05$ Mann-Whitney U-test).

2.5.1.4 Surface sculpturing

The surface sculpturing of *Brosimum* is finely scabrate, with the exception of *Brosimum gaudichaudii* which is psilate (Table 2.5-1; Figs 2.5-1 (D); Appendix 1). *Maquira coriacea*, *Maclura tinctoria*, *Helicostylis*, *Pourouma* and *Sorocea* are also finely scabrate, whilst the latter two species are coarsely scabrate (Fig. 2.5-1 (K - M)). *Pseudolmedia*, *Ficus*, and the Urticaceae species, *Urera caracasana* and *Pouzolzia poeppigiana*, are psilate.

2.6 Discussion

The following discussion is divided into two sections. The first focuses on the differentiation between key Moraceae pollen types of NKMNP and their ecological significance. The second section outlines implications for the interpretation of fossil pollen records at the local (NKMNP) and basin-wide spatial scales.

2.6.1 *Distinctive pollen types*

2.6.1.1 Helicostylis

Helicostylis can be readily distinguished from other pollen types. Its key diagnostic features are its size (P = 9.5 ± 0.8 μm; E = 12 ± 0.5 μm), number of pores (2-3), shape

class (P/E = 0.78; suboblate), and finely scabrate sculpturing (Table 2.5-1). It can be differentiated from the morphologically similar *Ficus* by its sculpturing and shape class (Fig. 2.5-1 (I-J, O); Appendix 1). *Helicostylis* is finely scabrate and has a suboblate shape class according to its P/E ratio. In contrast, *Ficus* is psilate and has a distinctly oblate shape class (mean P/E of 0.65). However, *Ficus* is rare in both modern and fossil pollen assemblages because it is cleistogamous (Bush and Riviera, 2001; see above). It is absent from pollen records of Laguna Bella Vista and Laguna Chaplin (Burbridge et al., 2004; Mayle et al., 2000), as well as from modern pollen traps in *terra firme* evergreen rainforest study plots of NKMNP (Gosling et al. 2005), even though it is abundant in the vegetation (Salvias Project database, 2007).

Within NKMNP, *Helicostylis* is well represented in moist evergreen *terra firme* rainforest (Importance Value Index; IVI = 4.5; Salvias Database, 2007), seasonally inundated rainforest (IVI = 6.2) and evergreen liana forest (IVI = 2.7). However, it is ecologically less important in riparian forest communities (IVI = 0.6). Its palynological importance across Amazonia is implied by its basin-wide geographic distribution (VAST, 2007; Fig. 2.6-1 (D)).

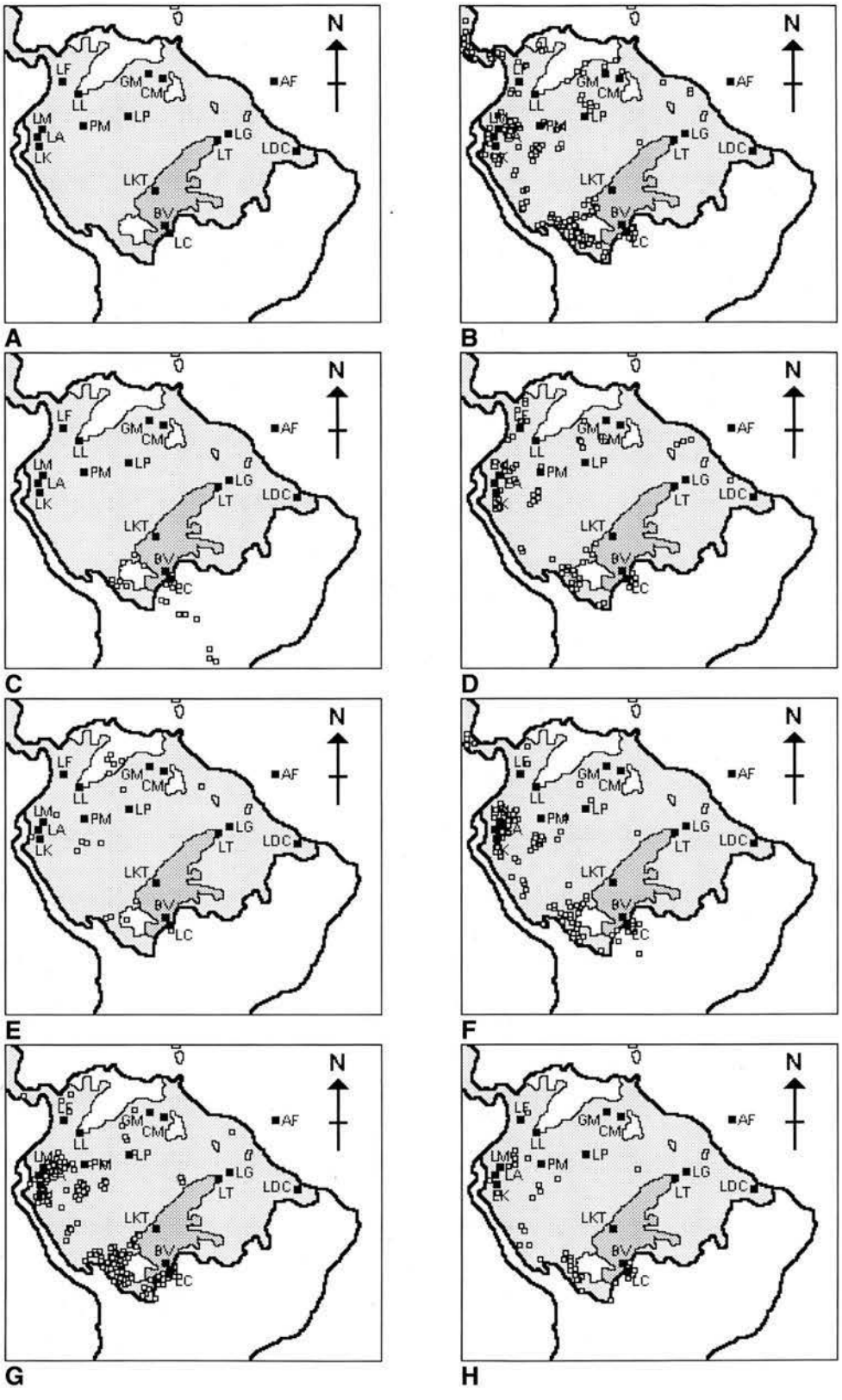
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Fig. 2.6-1: Geographic distribution of parent taxa of Moraceae pollen types differentiated in this paper (filled squares) plotted alongside the distribution of key Holocene and Lateglacial fossil pollen sites in the Amazon lowlands (open squares). The light grey area represents the Amazon Basin and the dark grey area the Madeira-Tapajós moist forest ecoregion. Mapped species are based on output from the VAScular Tropicos (VAST) Nomenclatural Database (2007) provided by the Missouri Botanical Gardens, and are indicative of the presence/absence of plants at specific sites. A: Fossil pollen sites: LF, Laguna Funza (Van't Veer and Hooghiemstra, 2000); LL, Laguna Loma Linda (Behling and Hooghiemstra, 2000); LM, (Liu and Colinvaux, 1985); LA, Laguna Ayauch (Bush and Colinvaux, 1988); LK, Laguna Kumpak (Liu and Colinvaux, 1988); PM, Pantano de Monica (Behling et al., 1999); LP, Lagoa Pata (Colinvaux et al., 1996); GM, Guaiquinima massif (Rull, 2005); CM, Chimanta Massif (Rull, 2005); LKT, Katira (Van der Hammen and Absy, 1994); BV, Laguna Bella Vista; LC, Laguna Chaplin (Burbridge et al., 2004; Mayle et al., 2000); LT, Lago Tapajós (Irion et al., 2006); LG, Lagoa Geral and Lagoa Comprida (Bush et al., 2000); LDC, Lagoa do Caço (Ledru et al., 2001); AF, Amazon Fan (Haberle and Maslin, 1999). B: *Brosimum alicastrum*, *B. guianense* and *B. lactescens*, C: *B. gaudichaudii*, D: *Helicostylis tomentosa* and *H. scabra*, E: *Maquira coriacea*, F: *Pourouma guianensis* and *P. minor*, G: *Pseudolmedia laevigata*, *P. laevis* and *P. macrophylla*, H: *Sorocea guilleminiana* and *S. hirtella*.

2.6.1.2 Brosimum

Brosimum is another key pollen type that is readily identifiable within NKMNP. Its constituent species, *Brosimum alicastrum*, *B. lactescens* and *B. guianensis,* are diporate, have P/E ratios that are distinctly spheroidal (P/E = 0.98 – 1.00), are finely scabrate, and have a distinct annulus surrounding the pores (Fig. 2.5-1 (A, B and C)). Furthermore, *B. alicastrum* and *B. lactescens* produce large grains with mean equatorial diameters and polar axis lengths measuring 18.5 ± 1 μm and 18 ± 1 μm, respectively. *B. guianensis* may be confused with *Sorocea* by its size and P/E ratio (Table 2.5-1), but can be distinguished from this taxon by the presence of its annulus (Appendix 1).

Brosimum species are late-successional and strongly represented in both riparian and seasonally flooded forest communities within NKMNP (Killeen, 1998) and across the Amazon Basin (VAST, 2007, Fig. 2.6-1 (B)). *B. lactescens*, for example, has an IVI of 38.6 within riverine forests and *B. guianensis* is represented in both riparian and inundated forest communities with an IVI of 3.42 and 5.3, respectively. Neither is represented in well-drained (*terra firme*) forest communities,

so abundance of their pollen in the fossil record would indicate that riparian and/or flooded forests were present in the catchment in the past.

The pollen of *B. gaudichaudii* (Fig. 2.5-1 (D)) is an interesting exception which can be readily differentiated from that of other *Brosimum* species by its shape classes (P/E = 1.21, subprolate; P/D = 1.36, prolate), psilate sculpturing and small size (mean equatorial diameter and polar axis length of 12 µm and 14.5 µm, respectively). Pollen grains of *B. gaudichaudii* and *Pourouma minor* are more difficult to distinguish from one another because they have a very similar shape classes (Table 2.5-1; Figs. 2.5-3 (a - b)). However, unlike *B. gaudichaudii*, *Pourouma minor* exhibits a thickening of the exine around the pores (Fig. 2.5-1 (L)) and is coarsely scabrate.

B. gaudichaudii is a shrub that grows in both cerradão (dense savanna woodland) and *cerrado* (upland savanna) communities of NKMNP (Killeen, 1998), as well as in seasonally-flooded savannas, both in Bolivia (*pampa termitera*) and Brazil (*murundus*) (Fig. 2.6-1 (C); De Oliveira-Filho, 1992). Presence of this pollen type therefore has implications for the interpretation of the Moraceae/Urticaceae signal within fossil pollen records in ecotonal regions of the Amazon Basin, such as Laguna Chaplin and Laguna Bella Vista (Fig. 2.3-1; Burbridge et al., 2004; Mayle et al., 2000).

2.6.1.3 Pseudolmedia and Maquira coriacea

Pseudolmedia and *Maquira* are difficult to distinguish from each other palynologically, although their pollen can be readily differentiated from that of other genera (Figs. 2.5-1 (E – G) and Appendix 1). *Pseudolmedia* pollen is 3-4 porate, psilate, angulaperturate, and relatively large, with a mean equatorial diameter and

polar axis length of 18.5 ± 2µm and 16.5 ± 2.5µm, respectively. *Maquira coriacea* is 3-4-5 porate, scabrate, angulaperturate and has a mean equatorial diameter and polar axis length of 18.5 ± 1 µm and 15.5 ± 0.5 µm (Fig. 2.5-1 (H)). Both can be differentiated from *Helicostylis* by their size, shape class and sculpturing (Table 2.5-1). If pollen preservation is poor, it may not be possible to reliably distinguish between 3-4 porate pollen grains of *Maquira coriacea* and *Pseudolmedia*. However, pentaporate grains can unequivocally be identified as *Maquira*, as pollen of all other taxa in this study have 4 pores or less (Table 2.5-1).

Pseudolmedia species are late-successional canopy trees that grow in both well-drained and inundated rainforest communities across the Amazon Basin (VAST, 2007; Fig. 2.6-1 (G)). This genus is particularly prominent in *terra firme* plots of NKMNP, where *P. laevis* and *P. macrophylla* have IVI values of 11.7 and 6.3, respectively. Abundant *Pseudolmedia* pollen in the fossil record would therefore be indicative of evergreen rainforest. *Maquira coriacea* is ecologically restricted to riparian evergreen forest communities within the Amazon Basin (Killeen, 1998; Nebel et al., 2001b; Fig. 2.6.1 (E)). It is especially important in riparian forests lining the Rio Paraguá (IVI = 29) and is not recorded in any other plant community in NKMNP. The presence of this taxon in fossil pollen assemblages would therefore provide strong evidence for riparian forest.

2.6.1.4 Pourouma, Sorocea and Maclura tinctoria

Pollen grains of *Pourouma*, *Sorocea* and *Maclura tinctoria* are rather more difficult to differentiate from each other (Fig. 2.5-1 (K – N, P)). It is, however, possible to separate them according to their P/D ratios (Figs. 2.5-2 (b); Appendix 1). *Pourouma minor* and *Pourouma guainensis* exhibit P/D ratios that are strongly prolate (P/D =

1.44 and 1.33, respectively) in contrast to those of *Sorocea* and *Maclura tinctoria*, which are subprolate.

Pourouma guianensis is a common tree in *terra firme* tall humid evergreen (IVI = 3.1) and liana forests (IVI = 3.5) in NKMNP. *P. minor* is less common, although Killeen (1998) reports its presence in gallery forests within the park and both species are present across the Amazon Basin (VAST, 2007; Fig. 2.6-1 (F)). *Sorocea* species inhabit a wide range of plant communities within NKMNP, albeit at low abundance; e.g. *S. guilleminiana* grows in both *terra firme* (IVI = 0.47) and seasonally-inundated (IVI = 2.8) rainforest communities, as well as in semi-deciduous dry forests and savannas, (Killeen, 1998). It too has a range extending across Amazonia (Fig. 2.6-1 (H)). *Maclura tinctoria* is adapted to a wide range of forest types extending from southern Mexico to northern Argentina (Marchant et al., 2002), and is present in NKMNP in evergreen liana forest (IVI = 0.42) and dry forest (Killeen, 1998), although it is uncommon. In summary, *Pourouma*, *Sorocea* and *Maclura tinctoria*, considered as a group, are indicative of a variety of forest types, and are therefore of lower palaeoecological value than other Moraceae genera.

2.6.1.5 Intra-species variability in aperture number

A number of fossil (Colinvaux et al. 1997; Bush et al. 2000) and modern pollen diagrams (Weng et al., 2004; Gosling et al. 2005) have sub-divided Moraceae/Urticaceae pollen solely on the basis of the number of apertures. The evidence presented here (Table 2.5-1; Figs. 2.5-1 (E, H, I, J)) demonstrates that, in general, such characterisation is of limited taxonomic value because several Moraceae genera have pollen with the same number of pores (e.g. *Brosimum, Ficus, Pourouma,* and *Sorocea* all have diporate pollen grains), whilst others have pollen

with variable pore number (e.g. *Pseudolmedia* spp.: 3-4 porate, *Maquira coriacea*: 3-4-5 porate, *Helicostylis* spp.: 2-3 porate, *Maclura tinctoria*: 2-3 porate). Use of pore number as a taxonomic criterion for this family is therefore best applied in conjunction with other diagnostic characters such as surface sculpture, pore characteristics, and grain shape.

2.6.2 *Palaeoecological implications*

2.6.2.1 Noel Kempff Mercado National Park

The ability to palynologically differentiate the constituent genera of Moraceae and Urticaceae means that there is now the potential for making more reliable and detailed palaeovegetation reconstructions than has hitherto been possible. As well as applying this increased taxonomic resolution to future fossil pollen studies of new sites, it is also fruitful to re-examine previously studied sites to improve upon, or at least test, earlier palaeoenvironmental reconstructions. The two most obvious sites for re-analysis of their Moraceae/Urticaceae pollen records are Laguna Chaplin and Laguna Bella Vista, since they are both located within the NKMNP study area, are surrounded by a mosaic of different kinds of rainforest, and reveal a 50,000 year record of rainforest-savanna dynamics (Fig. 2.3-1; Mayle et al., 2000; Burbridge et al., 2004). Differentiating between the different Moraceae/Urticaceae pollen types should reveal whether the late Holocene increase in abundance of this pollen type is due to development of *terra firme* rainforest or seasonally-flooded/riverine forest or a combination of the two. If the rise in Moraceae pollen at these sites is solely due to seasonally flooded/riparian genera, then this may point to local hydrological changes in the nearby river flood-plain, whereas expansion of genera from upland *terra firme*

rainforest would be more convincing evidence for a change to a wetter climate. Identification of pollen of *B. gaudichaudii* in the fossil record could be of even greater significance. Abundance of this taxon in the pollen record would challenge the assumption that abundance of Moraceae pollen is indicative of rainforest (Colinvaux and De Oliveira, 2000, Mayle et al., 2004; Gosling et al., 2005) because *B. gaudichaudii* is currently restricted to, and indicative of, rather more arid environments to the south of the Amazon Basin, including well-drained savanna (*cerrado*), open woodland (*cerradão*), and seasonally-flooded savanna (Fig. 2.6-1 (C); De Oliveira-Filho, 1992; Killeen, 1998; Marchant et al., 2002;). It is clear, therefore, that a taxonomic re-evaluation of the Moraceae/Urticaceae-type pollen of the fossil pollen assemblages of Laguna Chaplin and Laguna Bella Vista could potentially lead to palaeoclimatic inferences quite different from those previously made by the authors in the initial studies (i.e. Mayle et al., 2000; Burbridge et al., 2004).

2.6.2.2 Amazon Basin

It would seem reasonable to assume that the pollen-morphological differences revealed here, should hold true within the floristically-distinct Madeira-Tapajós moist forest ecoregion, which encompasses our study area (Fig. 2.3-1). For example, applying these results to the Rio Tapajós lake sediments (Fig. 2.6-1 (A); Irion et al., 2006), which lie within this ecoregion, could determine whether the Holocene rainforest signal at this site predominantly reflects local riparian rainforest bordering the river basin, or instead *terra firme* rainforest across a much larger area beyond the river basin.

The widespread geographic distribution of the taxa differentiated palynologically in this paper (Fig. 2.6-1), and the dominance of Moraceae pollen in all fossil pollen sites that have so far been studied in Amazonia (Mayle et al., 2004), clearly illustrates the importance of our findings for palaeoecology of the basin as a whole. It would be particularly useful to apply our findings to the previously-published Late Quaternary pollen records of the Amazon Fan (Haberle, 1997; Haberle and Maslin 1999), in order to help resolve the controversy over their significance for the Quaternary history of Amazonia's rainforests. Some have argued that the dominance of Moraceae/Urticaceae pollen throughout the glacial-Holocene sequence is evidence that Amazonia was largely covered by rainforest throughout this period (e.g. Haberle and Maslin 1999; Colinvaux et al., 2000), whereas others have suggested that it may simply reflect gallery or riparian forest lining the rivers during glacial periods, which masked pollen from savannas or dry forests beyond, consistent with the glacial aridity hypothesis (e.g. Haffer, 1969; Prado and Gibbs, 1993; Haffer and Prance, 2001; Pennington et al. 2000). If the glacial Moraceae/Urticaceae pollen signal was found to comprise predominantly riparian or seasonally-flooded rainforest species, such as *Brosimum lactescens*, *B. guianensis*, or *Maquira coriacea*, this would be strong evidence that the Amazon Fan pollen record primarily reflects riverine rainforests rather than *terra firme* vegetation beyond. In contrast, a glacial Moraceae pollen signal that was instead dominated by *Helicostylis* and/or *Pseudolmedia* would demonstrate a regional *terra firme* rainforest signal.

The diversity and importance of Amazonian genera of the Moraceae family has, until now, not been captured in fossil pollen records of the Amazon Basin. Our results suggest that ecosystem-specific indicator taxa of this family may be

differentiated from each other palynologically, and should therefore be used to improve the interpretation of fossil pollen records. These results will not only permit the palynological differentiation of different rainforest communities, but they will also improve our knowledge of the spatial extent of Amazonian rainforests during the Quaternary. Moreover, an improved understanding of the historical biogeography of the Amazon Basin would provide more precise estimates of past carbon storage, which may, in turn, provide invaluable data for the testing of climate and vegetation models.

2.7 Conclusions

An important limitation of previous Neotropical pollen studies is that pollen of the constituent genera of Moraceae and Urticaceae have not been differentiated from each other and have generally been considered as a single Moraceae/Urticaceae pollen type. In this study we examined pollen grains of each species of these two families recorded in NKMNP, NE Bolivia, measuring the following morphological features: shape and size of the grain, pore characteristics and number, and surface sculpture. When considering these parameters in combination, we find that it is possible to differentiate between pollen of the following taxa within the Moraceae family: *Helicostylis* spp., *Brosimum* spp, *Brosimum gaudichaudii*, *Pseudolmedia* spp., *Sorocea* spp., *Pourouma* spp., and *Maquira coriacea.* Furthermore, these Moraceae pollen types can be distinguished from Urticaceae pollen (*Urera* and *Pouzolzia*). This improved taxonomic resolution provides the potential for differentiating between different kinds of rainforest, especially riparian/seasonally-flooded rainforest *versus terra firme* rainforest, as well as potentially identifying

savanna/woodland (i.e. *Brosimum gaudichaudii*). Consequently, much more detailed palaeovegetation reconstructions can now be achieved for Amazonia than have hitherto been possible.

2.8 Appendix 1

A taxonomic key to pollen types of Moraceae and Urticaceae genera and species of NKMNP; terminology *sensu* Punt et al. (2007) and format *sensu* Roubik and Moreno (1991). **Pourouma* has been re-classified as Cecropiaceae in IPNI (2007).

1a. Diporate

2a. Grain Psilate
- 3a. P/E = 1.19-1.23 (subprolate) — *Brosimum gaudichaudii*
- 3b. P/E = 0.63-0.65 (oblate) — *Ficus citrifolia*, *Ficus pertusa*, *Ficus paraensis*

2b. Grain Finely Scabrate
- 4a. P/E = 0.98 - 1 (spheroidal)
  - 5a. Porus with a distinct annulus — *Brosimum alicastrum*, *Brosimum guianense*, *Brosimum lactescens*
  - 5b. Porus without annulus — *Sorocea hirtella*, *Maclura tinctoria*
- 4b. P/E = 0.76 – 0.79 (suboblate) — *Helicostylis scabra*, *Helicostylis tomentosa*

2c. Grain Coarsely Scabrate
- 6a. P/D = 1.34 – 1.44 (prolate) — *Pourouma minor**, *Pourouma guianensis**
- 6b. P/D = 1.16 – 1.2 (subprolate) — *Sorocea guilleminiana*

1b. Triporate

7a. Grain Psilate
- 8a. Grain angulaperturate — *Pseudolmedia laevigata*, *Pseudolmedia laevis*, *Pseudolmedia macrophylla*
- 8b. P/D = 0.85 – 0.86 (spheroidal) — *Urera caracasana*, *Pouzolzia poeppigiana*

7b. Grain Finely Scabrate
- 9a. Grain angulaperturate — *Helicostylis scabra*, *Helicostylis tomentosa*

9b. P/D = 1.16 (subprolate) — *Maclura tinctoria*

1c. Pantoporate (4-5 pores)

9a. 4-porate
10a. Grain Psilate — *Pseudolmedia laevigata*
Pseudolmedia laevis
Pseudolmedia macrophylla

10b. Grain Finely Scabrate — *Maquira coriacea*
9b. 5-porate — *Maquira coriacea*

Pollen Descriptions

Brosimum alicastrum Swartz
Diporate; sexine finely scabrate; pores 3 µm diameter; P = 17 – 20 µm, E = 16 – 20 µm, D = 15 – 18 µm; P/E = 1 (spheroidal); P/D = 1.09 (prolate-spheroidal).

Brosimum gaudichaudii Trécul
Diporate; sexine psilate; pores 1.5 – 2 µm diameter; P = 13 – 16 µm, E = 11 – 14 µm, D = 9 – 13 µm; P/E = 1.19 – 1.23 (subprolate); P/D = 1.35 – 1.37 (prolate).

Brosimum guianense (Aublet) Huber
Diporate; sexine finely scabrate; pores 1.5 – 2 µm diameter; P = 14 – 17 µm, E = 14 – 17 µm, D = 11 – 13 µm; P/E = 1 (spheroidal); P/D = 1.29 (subprolate).

Brosimum lactescens (Moore) C.C. Berg
Diporate; sexine finely scabrate; pores 3 µm diameter; P = 17 – 20 µm, E = 16 – 20 µm, D = 16 – 18 µm; P/E = 0.98 – 0.99 (spheroidal); P/D = 1.1 – 1.11 (prolate spheroidal).

Ficus citrifolia Miller
Diporate; sexine psilate; pores 1 – 1.5 µm diameter; P = 7 – 9 µm, E = 11 – 14 µm; P/E = 0.65 (oblate).

Ficus paraensis (Miquel) Miquel
Diporate; sexine psilate; pores 1 – 1.5 µm diameter; P = 8 – 10 µm, E = 13 – 16 µm; P/E = 0.64 (oblate).

Ficus pertusa Linnaeus
Diporate; sexine psilate; pores 1 – 1.5 µm diameter; P = 5 – 7 µm, E = 9 – 10 µm; P/E = 0.63 (oblate).

Helicostylis scabra (Macbride) C.C. Berg
Diporate and triporate; sexine finely scabrate; pores 1.5 µm diameter; amb angulaperturate; P = 7 – 12 µm, E = 11 – 13 µm; P/E = 0.78 (suboblate).

Helicostylis tomentosa (Poeppig & Endlicher) J.F. Macbride
Diporate and triporate; sexine finely scabrate; pores 1.5 µm diameter; amb angulaperturate; P = 8 – 10 µm, E = 11 – 13 µm; P/E = 0.76 – 0.79 (suboblate).

Maclura tinctoria Steudel
Diporate and triporate; sexine finely scabrate; pores 2 µm diameter; P = 11 – 13 µm, E = 11 – 13 µm, D = 9 – 12 µm; P/E = 0.99 amb (spheroidal); P/D = 1.16 (subprolate).

Maquira coriacea (Karsten) C.C. Berg
Diporate, triporate and pantoporate (4 and 5 pores); sexine finely scabrate; pores 2 µm diameter; amb angulaperturate; P = 15 – 17 µm, E = 17 – 20 µm; P/E = 0.84 (suboblate).

Pourouma guianensis Aublet Subsp. *guianensis*
Diporate; sexine coarsely scabrate; pores 1.5 µm diameter; P = 12 - 15 µm, E = 11 - 15 µm, D = 9 - 12 µm; P/E = 1.04 (spheroidal); P/D = 1.34 (prolate).

Pourouma minor Benoist
Diporate; sexine coarsely scabrate; pores 1.5 µm diameter; P = 13 -16 µm, E = 12 – 14 µm, D = 10 – 11 µm; P/E = 1.19 (subprolate); P/D = 1.44 (prolate).

Pouzolzia poeppigiana (Weddell) Killip
Triporate; sexine psilate; pores 1 – 1.5 µm diameter; amb spheroidal; P = 9 – 12 µm, E = 10 – 14 µm, P/E = 0.85 (suboblate).

Pseudolmedia laevigata Trécul
Triporate and 4-porate; sexine psilate; pores 2 µm diameter; amb angulaperturate; P = 11 – 15 µm, E = 14 – 18 µm; P/E = 0.84 (suboblate).

Pseudolmedia laevis (Ruiz & Pavon) J.F. Macbride
Triporate and 4-porate; sexine psilate; pores 2 – 3 µm diameter; amb angulaperturate; P = 15 – 21 µm, E = 17 – 22 µm; P/E = 0.92 (spheroidal).

Pseudolmedia macrophylla Trécul
Triporate and 4-porate; sexine psilate; pores 2 µm diameter; amb angulaperturate; P = 15 – 21 µm, E = 19 – 25 µm; P/E = 0.92 (spheroidal).

Sorocea guilleminiana Gaudichaud-Beaupré
Diporate; sexine coarsely scabrate; pores 2 µm diameter; P = 13 – 16 µm, E = 14 – 17 µm, D = 12 – 13 µm; P/E = 0.99 – 1.05 (spheroidal); P/D = 1.16 – 1.2 (subprolate).

Sorocea hirtella Mildbraed

Diporate; sexine finely scabrate; pores 2 µm diameter; P = 10 – 14 µm, E = 11 – 14 µm, D = 11 – 12 µm; P/E = 0.98 (spheroidal); P/D = 1.1 (prolate spheroidal).

Urera caracasana Grisebach
Triporate; sexine psilate; pores 1 – 1.5 µm diameter; amb spheroidal; P = 7 – 12 µm, E = 9 – 14 µm; P/E = 0.86 (suboblate).

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2.10 References

Anhuf, D., Ledru, M.P., Behling, H., Da Cruz Jr., F.W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J.A., De Oliveira, P.E., Pessenda, L., Siffedine, A., Albuquerque, A.L. and Da Silva Dias, P.L. (2006). Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeography, Palaeoclimatology, Palaeoecology* **239**, 510-527.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D. and Broda, J.P. (2001). The history of South American tropical precipitation for the past 25,000 years. *Science* **291**, 640-643.

Beerling, D.J. and Mayle, F.E. (2006).Contrasting effects of climate and CO_2 on Amazonian ecosystems since the last glacial maximum. *Global Change Biology* **12**, 1977-1984.

Behling, H., Berrio, J. and Hooghiemstra, H. (1999). Late Quaternary pollen records from the middle Caqueta river basin in central Colombian Amazon. *Palaeogeography, Palaeoclimatology, Palaeoecology* **145**, 1, 193-213.

Behling, H. (2002). Carbon storage increases by major forest ecosystems in tropical South America since the Last Glacial Maximum and the early Holocene. *Global and Planetary Change* **33**, 107-116.

Behling, H. and Hooghiemstra, H. (2000). Holocene Amazon rainforest-savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Columbia. *Journal of Quaternary Science* **15**, 687-695.

Burbridge, R.A., Mayle, F.E. and Killeen, T.J. (2004). Fifty-thousand year vegetation and climate history of noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* **61**, 215-230.

Bush, M.B. (2002). On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177**, 5-17.

Bush, M.B. and Colinvaux, P.A. (1988). A 7000-year record from the Amazon lowlands, Ecuador. *Vegetatio* **76**, 141-154.

Bush, M.B. and Riviera, R. (2001). Reproductive ecology and pollen representation among Neotropical trees. *Global Ecology and Biogeography* **10**, 359-367.

Bush, M.B., de Oliveira, P.E., Colinvaux, P.A., Miller, M.C. and Moreno, J.E. (2004). Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214**, 359-393.

Bush, M.B., Miller, M.C., De Oliveira, P.E. and Colinvaux, P.A. (2000). Two histories of environmental change and human disturbance in eastern lowland Amazonia. *The Holocene* **10**, 5, 543-553.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C. and Bush, M.B. (1996). A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* **274**, 85-88.

Colinvaux, P.A. and de Oliveira, P.E. (2000). Palaeoecology and climate of the Amazon basin during the last glacial cycle. *Journal of Quaternary Science* **166**, 51-63.

Colinvaux, P.A., De Oliveira, P.E. and Bush, M.B. (2000). Amazonian and Neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19**, 141-169.

Cowling, S.A., Betts, R.A., Cox, P.M., Ettwein, V.J., Jones, C.D., Maslin, M.A. and Spall, S.A. (2005). Modelling the past and future fate of the Amazonian forest. In

Malhi, Y. and Phillips, O. (Eds.), Tropical forests and global atmospheric change. Oxford University Press, Oxford, 191-198.

Datwyler, S.L. and Weiblen, G.D. (2004). On the origin of the fig: Phylogenetic relationships of Moraceae from *ndhF* sequences. *American Journal of Botany* **91**, 767-777.

De Oliveira-Filho A.T. (1992). The vegetation of Brazilian 'murundus' – the island-effect on the plant community. *Journal of Tropical Ecology* **8**, 4, 465-486.

Erdtman, G., 1943. An introduction to pollen analysis. Chronica Botanica, Waltham, Massachusetts.

Faegri, K. and Iversen, J. (1989). Textbook of pollen analysis. Blackburn Press, New Jersey.

Gosling, W.D., Mayle, F.E., Tate, N.J. and Killeen, T.J. (2005). Modern pollen-rain characteristics of tall *terra firme* moist evergreen forest, southern Amazonia. *Quaternary Research* **64**, 284-297.

Haberle, S. (1997). Upper Quaternary vegetation and climate history of the Amazon Basin: Correlating marine and terrestrial pollen records. In Flood, R.D., Piper, D.J.W., Klaus, A. and Peterson, L.C., (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 155: College Station, TX.

Haberle, S.G. and Maslin, M.A. (1999). Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon Fan, ODP site 932. *Quaternary Research* **51**, 27-38.

Haffer, J. and Prance, G.T. (2001). Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* **16**, 579-607.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165**, 131-137.

International Plant Names Index (2007). Published on the Internet http://www.ipni.org [accessed 9 January 2007].

Irion, G., Bush, M.B., Nunes de Mello, J.A., Stüben, D., Neumann, T., Müller, G., Morais de, J.O. and Junk, J.W. (2006). A multiproxy palaeoecological record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **240**, 523-535.

Killeen, T.J. (1998). Vegetation and flora of Parque Nacional Noel Kempff Mercado. In Killeen, T.J. and Schulenberg, T.S. (Eds.), A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP Working Papers 10, Conservation International, Washington D.C. 61-85.

Killeen, T.J. and Schulenberg, T.S. (1998). A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP Working Papers 10, Conservation International, Washington D.C.

Killeen, T.J., Siles, T.M., Grimwood, T., Tieszen, L.L., Steininger, M.K., Tucker, C.J., and Panfil, S. (2003). Habitat heterogeneity on a forest-savanna ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): Implications for the long-term conservation of biodiversity in a changing climate. In Bradshaw, G.A. and Marquet, P.A. (Eds.), How landscapes change: Human disturbance and ecosystem fragmentation in the Americas, *Ecological Studies* **162**, Springer Verlag, Berlin.

Ledru, M., Cordeiro, R.C., Dominguez, J.M.L., Martin, L., Mourguiart, P. and Siffedine, A. (2001). Late-Glacial Cooling in Amazonia Inferred from Pollen at Lagoa do Caco, Northern Brazil. *Quaternary Research* **55**, 47–56.

Liu, K. and Colinvaux, P.A. (1985). Forest changes in the Amazon Basin during the last glacial maximum. *Nature* **318**, 556-557.

Liu, K. and Colinvaux, P.A. (1988). A 5200-year history of Amazon rain forest. *Journal of Biogeography* **15**, 231-248.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., De Oliveira-Filho, A.T., Lozano-Garćia, S., Hooghiemstra, H., Ledru, M., Ludlow-Wiechers, B., Markgraf, V.,

Mancini, V., Paez, M., Prieto, A., Rangel, O. and Salgado-Labouriau, M.L. (2002). Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review of Palaeobotany and Palynology* **121**, 1-75.

Mayle, F.E. and Beerling, D.J. (2004). Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214**, 11-25.

Mayle, F.E., Beerling, D.J., Gosling, W.D. and Bush, M.B. (2004). Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society London B* **359**, 499-514.

Mayle, F.E., Burbridge, R.E. and Killeen, T.J. (2000). Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**, 2291-2294.

Nebel, G., Dragstad, J., Simonsen, T.R. and Vanclay, J.K. (2001b). The Amazon flood plain forest tree *Maquira coriacea* (Karsten) C.C. Berg: aspects of ecology and management. *Forest Ecology and Management* **150**, 130-113.

Nebel, G., Kvist, L.P., Vanclay, J.K., Christensen, H., Freitas, L. and Ruiz, J. (2001a). Structure and floristic composition of flood plain forests in the Peruvian Amazon I. *Overstorey. Forest Ecology and Management* **150**, 27-57.

Olsen, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Louks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* **51**, 933–938.

Orozco-Segovia, A., Vázquez-Yanes, C., Coates-Estrada, R. and Pérez-Nasser, N. (1987). Ecophysiological characteristics of the seed of the tropical forest pioneer *Urera caracasana* (Urticaceae). *Tree Physiology* **3**, 375-386.

Pennington, R.T., Prado, D.E. and Pendry, C.A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27**, 261-273.

Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S. and Le Thomas, A. (2007). Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology* **143**, 1-81.

Roubik, D.W. and Moreno, J.E. (1991). Pollen and Spores of Barro Colorado Island. *Monographs in Systematic Botany from the Missouri Botanical Garden* **36**, 1-268.

Rull, V. (2005). Palaeovegetational and palaeoenvironmental trends in the summit of the Guaiquinima massif (Venezuelan Guayana) during the Holocene. *Journal of Quaternary Science* **20**, 2 135-145.

Rull, V. (2005). Vegetation and environmental constancy in the Neotropical Guayana Highlands during the last 6000 years? *Review of Palaeobotany and Palynology* **135**, 205-222.

Sakai, S. (2001). Thrips pollination of androdioecious *Castilla Elastica*, (Moraceae) in a seasonal tropical forest. *American Journal of Botany* **88**, 1527-1534.

SALVIAS Project (2006). Published on the Internet http://www.salvias.net [accessed 9 December 2006].

Valdes, P.J. (2000). South American palaeoclimate model simulations: how reliable are the models? *Journal of Quaternary Science* **15**, 357-368.

Van der Hammen, T. (1974). The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* **1**, 3-26.

Van der Hammen, T. and Absy, M.L. (1994). Amazonia during the last glacial. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**, 247–261.

Van't Veer, R. and Hoogiemstra, H. (2000). Montane forest evolution during the last 650 000 yr in Colombia: a multivariate approach based on pollen record Funza-I. *Journal of Quaternary Science* **15**, 4, 329-346.

Vascular Tropicos Nomenclatural Database (2007). Published on the internet

http://mobot.mobot.org/W3T/Search/vast.html [accessed 8 January 2007].

Weng, C., Bush, M.B. and Silman, M.R. (2004). An analysis of modern pollen rain on an elevational gradient in southern Peru. *Journal of Tropical Ecology* **20**, 113-124.

Chapter 3 Palynological characterisation of Amazonian rainforest communities, Northeast Bolivia

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3.1 Abstract:

An ongoing controversy in Neotropical Palaeoecology is the extent to which Amazonian rainforest communities have responded to climate change over the last glacial-interglacial cycle. Progress can be made in this field by establishing characteristic pollen signatures for different types of rainforest community, comparing these with the fossil pollen record, and thereby extracting more detailed ecological information from the Quaternary sedimentary record. Using multivariate and cluster analyses applied to modern-pollen and floral-biometric data obtained from study plots situated within different rainforest communities of the Noel Kempff Mercado National Park (NKMNP; Madeira-Tapajós moist forest ecoregion), Northeast Bolivia, we show that *terra firme* (well-drained) evergreen, *terra firme*

liana, seasonally inundated, and riparian rainforests are readily characterised and differentiated by their pollen rain. Analogue matching techniques, based on Euclidean distance measures, are employed to compare numerically the resulting pollen signatures with surface sediment pollen assemblages taken from two lakes, Laguna Bella Vista and Laguna Chaplin, within NKMNP, and from three others: Laguna Huachi, surrounded by *terra firme* rainforest of the Madeira-Tapajós moist forest ecoregion west of NKMNP, and Lagunas San Ignacio and Loma Suarez, which are situated within gallery rainforests lining the Rio Mamoré of the Llanos de Moxos (Beni Basin) ecoregion.

Pollen signatures of riparian forest communities of NKMNP represent the closest modern analogue pollen assemblage to surface sediment samples from Lagunas Bella Vista and Chaplin; however, elements of *terra firme* forests also constitute a significant proportion of these assemblages. This result succesfully identifies the riparian and *terra firme* rainforest communities surrounding the two lakes today. Close similarity of modern pollen spectra obtained from lakes and traps within NKMNP with surface samples obtained from Laguna Huachi demonstrates consistency of rainforest pollen signatures within the Madeira-Tapajós ecoregion. Pollen spectra obtained from surface sediment samples from lakes situated within gallery forests of the Llanos de Moxos (Beni Basin) ecoregion are significantly different to those obtained from the Madeira-Tapajós ecoregion. Our ability to distinguish riparian and *terra firme* rainforests within fossil pollen assemblages has significant implications for the interpretation of important Quaternary pollen records across the Amazon Basin, including those from Lake Pata and the Amazon Fan,

which, in turn, has implications for our understanding of the response of Amazonian rainforests to climate change over the last glacial-interglacial cycle.

Key Words: *Terra firme* Rainforest, riparian rainforest, pollen rain, Madeira-Tapajós, Multivariate ordination, Cluster analysis, Amazon Basin.

3.2 Introduction

Amazonian rainforests are complex ecosystems that are heterogeneous across the Amazon Basin in terms of their structure and floristic composition as well as their carbon storage capacity (Tian et al., 1998; ter Steege et al., 2006). They are the most biodiverse ecosystems on earth (Morley, 2000; Willis and McElwain, 2002) and much of the 5.6 million km^2 area they inhabit remains in a relatively pristine condition. Diversity between rainforest habitats (beta-diversity) is very high resulting in a rich mosaic of communities that reflect underlying physical controls such as edaphic conditions, successional stage, and hydroperiod. *Terra firme* (non-flooded) evergreen rainforests are the most species rich comprising drought-adapted liana forests as well as moist evergreen tall forests. Seasonally-inundated forests are periodically flooded by blackwater rivers (igapó forests) or whitewater rivers (*várzea* forests) that drain the Precambrian Shield and the Andes mountains, respectively (Sioli 1968; Prance 1979, 1989). Seasonally-inundated and riparian forest communities are notably less species-rich, and smaller in stature, than *terra firme* forests (e.g. Duivenvoorden, 1996; Nebel et al., 2001a) as a result of geomorphological disturbance caused by hydrological changes of meandering rivers and because many species are unable to tolerate flooded conditions.

The spatial and floristic heterogeneity exhibited by Neotropical lowland rainforests has not been recognised within rainforest pollen assemblages of

Quaternary sedimentary records of the Amazon Basin (Colinvaux et al., 1996; Bush et al., 2004; Van der Hammen and Absy, 1994; Mayle et al., 2000; Haberle and Maslin, 1999). Indeed, considerable controversy surrounds the interpretation of these records, which hampers progress in our understanding of Quaternary vegetation dynamics (Colinvaux and DeOliveira, 2000; Pennington et al., 2000; Bush et al., 2004; Bush 2002; Anhuf et al., 2006; Mayle et al., 2004), the testing of climate and vegetation models (Valdez, 2000; Cowling et al., 1999; Cowling et al., 2001; Cowling et al., 2005) and in obtaining improved estimates of past carbon storage (Behling, 2002; Mayle and Beerling, 2004; Beerling and Mayle, 2006). Such controversy results, to a large extent, from our current inability to identify key Amazonian pollen types to a sufficient taxonomic resolution as well as a dearth of modern pollen-vegetation studies that attempt to characterise and differentiate the pollen rain assemblages of different rainforest communities (Bush et al., 2004; Gosling et al., 2005; Weng et al., 2004).

The ability to differentiate between pollen spectra of different rainforest communities is essential if more detailed palaeoecological reconstructions are to be made. For example, if a given fossil rainforest pollen assemblage is demonstrably of a riparian forest provenance, this would imply that the sedimentary record only records a local riparian rainforest signal. In contrast, if such an assemblage was shown to be of a *terra firme* upland forest provenance, this would reflect pollen deposition from upland areas distant from the shoreline. Such a distinction is of particular importance for our understanding of glacial fossil pollen assemblages recorded in sediments of the Amazon Fan (Haberle 1997; Haberle and Maslin, 1999) and at Lake Pata (Colinvaux et al., 1996). If these assemblages were shown to be

characteristic riparian forest signatures that line rivers of the Amazon Basin and mask other plant communities beyond, this would be consistent with both the continuous forest hypothesis (Colinvaux et al., 2000) and the glacial aridity hypothesis (Haffer, 1969; Prado and Gibbs, 1993; Van der Hammen and Absy, 1994; Haffer and Prance, 2001; Pennington et al., 2000). Conversely, a *terra firme* moist forest pollen signal would reflect spatially more extensive upland rainforests, support the continuous forest hypothesis of Colinvaux et al., (2000) and contradict the glacial aridity hypothesis. The palynological differentiation of liana rainforest communities also has implications for palaeoecological interpretations. Liana rainforests are most prevalent in the seasonal regions of the Amazon Basin (e.g. NE Bolivia) and exhibit lower biomass than tall moist forest communities. Evidence of liana forest expansion within the palaeoenvironmental record could therefore point to reduced precipitation as well as a reduced carbon store.

Here, we analyse the pollen rain sampled from multiple permanent plots situated within four different types of rainforest community of the Noel Kempff Mercado National Park (NKMNP), Northeast Bolivia, which represent two *terra firme* (moist evergreen rainforest and liana rainforests) and two seasonally flooded rainforests (seasonally inundated and riparian forests). Our aims are (1) to characterise and differentiate between the four distinct rainforest communities of NKMNP by their pollen rain; (2) to compare these pollen signatures numerically with floristic inventories obtained from forest plots to understand better the pollen-vegetation relationships of these rainforests; (3) to compare numerically pollen rain spectra with lake sediment samples within the park to test the applicability of artificial pollen trap data to Quaternary lake sediment records; and (4) to test the

extent to which pollen rain of NKMNP rainforests is consistent within the Madeira-Tapajos moist forest ecoregion and distinct from gallery forests of the Llanos de Moxos (Beni Savanna) ecoregion.

3.3 Study Area

Noel Kempff Mercado National Park (NKMNP) is a 15,230 km^2 biological reserve in northeast Bolivia that occupies part of the Madeira-Tapajós ecoregion (Olsen et al., 2001; Fig. 3.3-1). The park is situated on an ecotone spanning 22 largely pristine plant communities, from moist evergreen rainforest in the north, to *cerrado* (well-drained savanna) in the east, and semi-deciduous dry-forest communities in the south, and provides a physical setting that supports considerable ecosystem diversity (beta diversity; Killeen et al., 2003). Two black-water rivers, the Río Iténez and Río Paraguá define the eastern and western boundaries of NKMNP, respectively. Precambrian rocks of the Huanchaca Plateau (600-900 m a.s.l.) characterise the eastern half, and Tertiary alluvial deposits of the lowland peneplain (200-250 m a.s.l.), the western half of the park.

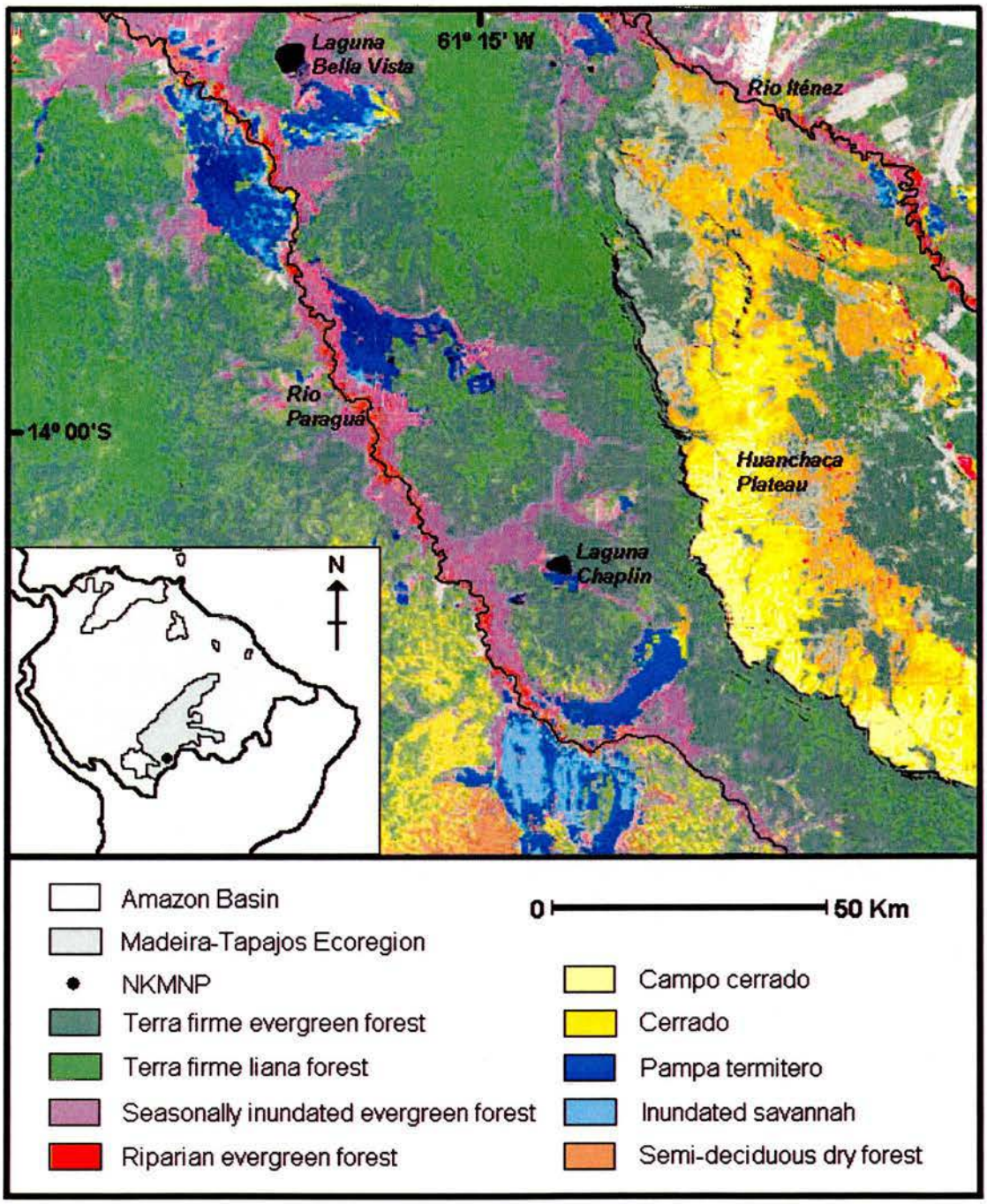

Fig. 3.3-1: Location map (inset) and distribution of plant communities within Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. Modified from Killeen and Schulenberg (1998). Black dots indicate the location of 1 hectare plots from which the floristic and pollen rain data was obtained.

The vegetation of the Huanchaca Plateau consists mainly of *cerrado* savanna communities, which are well-adapted to Oxisols that have developed on the basement rocks of the Precambrian Shield. Here, moist evergreen gallery forest is confined to valleys or depressions where water availability is sufficient (Killeen, 1998). In contrast, a variety of evergreen rainforest communities dominate the neighbouring alluvial plains. High evergreen rainforest and liana forest grow on well-drained (*terra firme*) Oxisols that have developed on Tertiary sediments, while riparian and seasonally inundated rainforests, as well as seasonally flooded savannas, develop on hydromorphic Entisols deposited during overbank flow of the Río Paraguá in the wet season (Killeen, 1998).

The Llanos de Moxos ecoregion (Beni Basin; Fig. 3.3-2) is a 160,000 km^2 area of seasonally inundated savannah that is truncated by the Río Mamoré and interspersed with forest islands occupying the higher ground. It forms part of the flat Beni-Mamoré-Iténez basin in Southwest Amazonia and is flanked by the Precambrian shield to the east and the Andes to the West. White-water rivers transporting fine sediments eroded from the Andes traverse the basin and numerous flat-bottomed lakes cover the landscape (Mayle et al., 2007). Floodplains of Río Mamoré are lined with tropical gallery forests and oxbow lakes formed by channel avulsion are plentiful. The floristic composition of these gallery forests is significantly different to the riparian forest of NKMNP and is characterised by the abundance of herbaceous and shrub pioneer species including *Tessaria integrifolia* (Asteraceae), *Gymerium sagittatum* (Poaceae), *Salix humboldtiana* (Salicaceae),*Cecropia membranacea* (Cecropiaceae) and *Alchornea castaneifolia* (Euphorbiaceae; Maldonando and Beck, 2004). The forests themselves are

predominantly characterised by the tree species *Ficus insipida* (Moraceae), *Inga* Spp. (Fabaceae), *Hura crepidans* (Euphorbiaceae) *Pourouma* spp., *Erythrina poeppigiana* and *Sapium marmieri* (Maldonando and Beck, 2004).

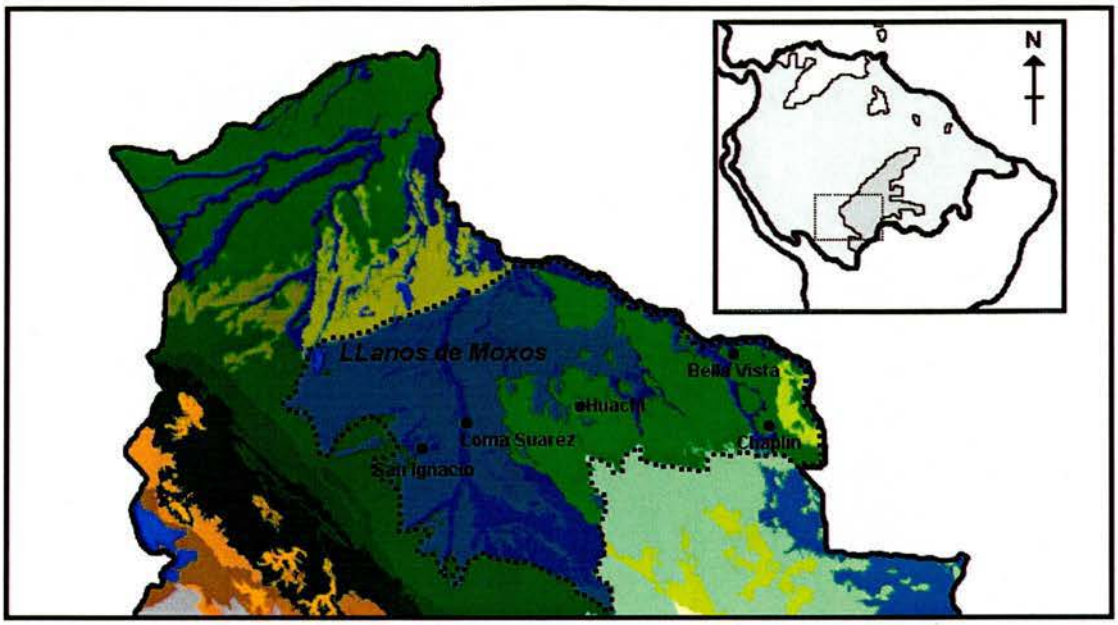

Fig. 3.3-2: Location map (inset) and distribution of ecoregions in northern Bolivia (After Olsen et al., 2001). The study area (within dotted line) comprises the Llanos de Moxos (Beni Savanna) ecoregion to the west and a part of the Madeira-Tapajós moist forest ecoregion to the east (light-green). Large black dots represent the location of lakes from which surface sediment samples were obtained.

Fig. 3.3-2 also shows the location of the five lakes from which surface samples were obtained. Laguna Chaplin (14° 28' S, 61° 04' W) and Laguna Bella Vista (13° 37' S, 61° 33' W), both situated within the Madeira-Tapajós moist forest ecoregion have revealed changes in vegetation, fire dynamics, and climate, over the last 50,000 years (Burbridge et al., 2004; Mayle et al., 2000; Fig. 1) and are situated within a mosaic of *terra firme*, riparian and seasonally inundated forest communities. Laguna Huachi (14°17' S, 63°23' W) is situated outside the park but within *terra firme* rainforests at the western most extent of the Madeira-Tapajós moist forest ecoregion. Laguna Loma Suarez (14°50' S, 64°54' W) is an oxbow lake situated

within gallery rainforests inhabiting the floodplains of the Rio Mamoré and Laguna San Ignacio (14°59' S, 63°41' W) lies within rainforest surrounded by Beni savannas. The floristic composition of forests surrounding both lakes is described above.

3.4 Methodology

3.4.1 *Field Techniques*

Detailed floristic inventories were obtained from one hectare (500 × 20 m) permanent study plots from 32 plant communities within NKMNP between 1993 and 2000 by Killeen (1998) and are readily available from the Salvias Project Database (2007). Two plots were set up for each of the studied communities and installed in visually homogeneous forest in order to minimize intra-plot heterogeneity. Every woody plant ≥ 10 cm d.b.h. (diameter at breast height) was measured and all tagged specimens were stored at the herbarium of the Museo de Historia Natural Noel Kempf Mercado in Santa Cruz, Bolivia. Identification was made by comparison with specimens held in the collection in Santa Cruz and at the Missouri Botanical Gardens (Killeen and Schulenberg, 1998). Standardized nomenclature is in accordance with publications cited in the International Plant Names Index (2007), a combination of Index Kewensis, the Gray Card Index and the Australian Plant Names Index. Our study employs floristic data obtained from eight of these plots situated within four different rainforest communities. The plots are representative of a wide range of rainforest communities found within the Amazon Basin and are presented in Table 3.4-1.

Table 3.4-1: Site characteristics of the eight studied rainforest plots within the Noel Kempff Mercado National Park (NKMNP). Floristic inventories were prepared for each of these sites (Salvias Database, 2007) and pollen signatures were previously obtained from Los Fierros 1 by Gosling (2004)

Name	Coordinates	Ecosystem	Plant Community	Size (m)
Las Londras 1	14°24'15"S; 61° 08'38"W	Moist inundated evergreen forest	Tall inundated evergreen forest	500x20
Las Londras 2	14° 24'15"S; 61° 08'38"W	Moist inundated evergreen forest	Tall inundated evergreen forest	500x20
Monte Cristo 1	14° 39'52"S; 61° 09'32"W	Moist inundated evergreen forest	Tall riverine evergreen forest	200x20
Monte Cristo 2	14° 42'36"S; 61° 09'21"W	Moist inundated evergreen forest	Tall riverine evergreen forest	500x20
Los Fierros 1	14° 34'50"S; 66° 49'48"W	Moist *terra firma* evergreen forest	Tall *terra firma* evergreen forest	500x20
Los Fierros 2	14° 34'50"S; 66° 49'48"W	Moist *terra firma* evergreen forest	Tall *terra firma* evergreen forest	500x20
El Chore 1	14° 23'08"S; 61° 8'52"W	Moist *terra firma* evergreen forest	*terra firma* liana forest	500x20
El Chore 2	14° 20'35"S; 61° 9'37"W	Moist *terra firma* evergreen forest	*terra firma* liana forest	500x20

All eight rainforest plots were sampled annually for pollen rain between September 1998 and September 2001 using artificial funnel pollen traps containing a rayon staple trapping medium (Gosling et al., 2003). Over this three year period, pollen rain was collected from two plots within each forest type to determine the degree of spatial and temporal consistency of pollen spectra both within a given type of rainforest, and between different types of rainforest. Traps were mounted on a stake 0.5 m above the ground or 0.5 m above the maximum level of inundation in seasonally-flooded communities (Gosling et al., 2003), determined by the strand-line on tree trunks. Five traps were positioned 100 m apart along the centre of each plot in order that the full spectrum of pollen rain was captured. After collection, the viscose

rayon fibre was separated from the funnel pollen traps, sealed in a plastic grip-lock bag and stored in a dark cold store below 3 °C to prevent microbial activity.

In July 2006, surface samples were obtained from the sediment-water interface of lakes situated within different rainforest communities of two ecoregions: Laguna Huachi within the Madeira-Tapajós moist forest ecoregion and Laguna Loma Suarez and Laguna San Ignacio within gallery forests of the Llanos de Moxos ecoregion (Beni Basin; Fig. 3.3-2). Using a clear Perspex tube and a piston, the uppermost 1 cm of sediment below the sediment-water interface was extruded into a plastic bottle and subsequently stored in the laboratory below 3°C. Surface samples from Laguna Bella Vista and Laguna Chaplin (Madeira-Tapajós moist forest ecoregion) were collected in the same manner, in 1995 and 1998, respectively (Burbridge et al., 2004; Mayle et al., 2000).

3.4.2 *Pollen preparation and counting*

Tablets containing *Lycopodium clavatum* spores were added to the samples in order to calculate total pollen accumulation rates (grains cm^{-2} yr^{-1}) accurately for the artificial trap samples and concentration (grains cm^{-3}) for the lake surface sediment samples (Maher, 1981; Stockmarr, 1971). The viscose rayon fibre and *Lycopodium* blend was suspended in 10 % NaOH for a few hours to soften the material and extract any humic acids. After rigorous mixing, the resulting slurry was placed on a 250μm sieve and washed with distilled water until 1 litre of liquid was recovered. The resulting filtrate was centrifuged and prepared for light microscopy following the standard methods of Faegri and Iverson (1989). Lake surface sediment samples were prepared with the standard KOH, HF and acetolysis methods of Faegri and

Iverson (1989). All residues were suspended in silicone oil and counted at ×400 and ×1000 magnification under an Olympus BX 40 light microscope. A total of 3000 pollen grains were counted for each forest community at Los Fierros (moist evergreen *terra firme* forest), Las Londras (moist evergreen seasonally-flooded forest) and Monte Cristo (moist evergreen riparian forest) and 2500 grains were counted at El Chore (evergreen liana forest). These are aggregate counts comprising 500 grains per annum per plot (5 traps with 100 grains counted per trap), over 3 years (500 x 3 years), and two plots per forest community (1500 x 2) (N.B. One year's data are missing from one of the El Chore plots, reflecting the lower pollen sum for this community). A total of 300 terrestrial pollen grains were counted for each of the surface sediment lake samples. Pollen identification was carried out to the finest possible taxonomic resolution using the modern pollen reference collection at the University of Edinburgh (over 1000 species), published pollen floras (Roubik and Moreno, 1991; Colinvaux et al., 1999), and the Neotropical Pollen Database (Bush and Weng, 2007). Identification was performed conservatively to ensure taxonomy had no adverse impact on numerical analyses. The final pollen dataset consisted of 120 pollen types of which 78 were identified.

3.4.3 *Numerical Analyses*

Prior to numerical analysis, all data matrices obtained from floristic inventories, pollen trap and surface sediment counts were square-root transformed in order to minimize the effect of over-represented taxa and to optimize the 'signal' to 'noise' ratio (Birks, 1986; Prentice, 1980). Proportional values were used in all cases because they stabilize the variance in the data (Birks and Gordon, 1985; Bennet and

Hicks, 2005). Relative density ((number of individuals of species/total number individuals)*100) was calculated for each species represented within the floristic inventory of the studied rainforest plots. Species were subsequently ranked in order of decreasing importance according to their relative abundance. Similarity between taxon assemblages of different plots was measured using the robust and widely applied metric coefficient of squared Euclidean distance (Oksanen et al., 2007; Kent and Coker, 1994). These distances were chosen because they are easily represented in geometric space in ordination analyses (e.g. Principal Components Analysis) and are ecologically meaningful for the analysis of sites representing short ecological gradients (Legendre and Gallagher, 2000; Lepš and Šmilauer, 2003). Calculations were carried out using the Community Ecology Package version 1.8-5 (Oksanen et al., 2007) available as freeware in R (R Development Core Team, 2007).

Multivariate and cluster analysis was applied to investigate the major gradients of variability in both the vegetation and pollen rain datasets and to group distinct rainforest communities and pollen assemblages into classes according to their taxonomic composition. Data were first analysed using Detrended Correspondence Analysis (DCA) to measure the gradient length in community composition (beta-diversity). Both datasets exhibited a gradient length of less than two standard deviation units, so the linear unconstrained Principal Components Analysis (PCA) was deemed to be sufficient for subsequent analyses. A PCA was applied to each of the covariance and correlation matrices of floristic and pollen datasets, to detect any structure or patterns within them and to assess the relative contribution of important taxa to the variance in the datasets. Classification of the data was performed using the Unweighted Pair Group with Arithmetic Mean

(UPGMA) agglomerative classification technique, an algorithm that iteratively fuses the two nearest clusters (or group of species) until only one cluster remains (Sneath and Snokal, 1973). Here, fusion between clusters is based on the smallest mean pairwise Euclidean distance between taxa.

The extent to which the structure in the pollen rain data is controlled by the distribution of species within the surrounding rainforests was investigated using direct ordination by means of canonical correspondence analysis (CCA; ter Braak 1986). Within a CCA the ordination axes are related to linear combinations of the explanatory variables (i.e. species recorded in floristic inventories) and variance in the pollen rain data is therefore constrained by the distribution of species within the studied forest plots. The species used to constrain the pollen data were selected according to their importance in driving the differentiation of plots as determined by results of PCAs on the covariance matrices of both floristic and pollen datasets. Datasets were harmonized to the same taxon list and the statistical significance of the relationship between selected trees and pollen rain was assessed using a permutation test (Oksanen et al. 2007). A partial CCA was applied to test the effect of the removal of selected genera from the analysis in order to better understand their importance for determining the variance within the pollen data.

Finally, a PCA and UPGMA cluster analysis were performed on the covariance matrices of pollen rain and lake surface-sediment pollen spectra to test the potential for pollen trap spectra to provide 'modern-analogue' datasets for comparison with the fossil pollen record.

3.5 Results

3.5.1 *Floristic data*

A total of 240 genera comprising 688 species were identified within the four rainforest communities (Salvias Database, 2007). *Terra firme* forests growing on well-drained soils were the most species-rich with forests at El Chore (*terra firme* liana forest) and Los Fierros (*terra firme* evergreen forest) comprising 229 and 182 species ha^{-1}, respectively. The seasonally-inundated and riparian forest communities, at Las Londras and Monte Cristo were less species-rich, comprising 144 and 133 species ha^{-1}, respectively. Only 17 of the 240 genera (7%) were present in all four communities demonstrating that these different types of rainforest are floristically distinct from one another, and that the studied rainforests are strongly heterogeneous at the beta-diversity level. A summary of key genera (relative cover > 1%) recorded at each of the four rainforest communities and ranked according to decreasing abundance is provided in Table 3.5-1. *Phenakospermum* (Strelitziaceae) and *Pseudolmedia* (Moraceae) dominate the *terra firme* forest communities at Los Fierros. The Vochysiaceae family is well-represented by *Qualea*, *Erisma* and *Vochysia* and the genera *Euterpe*, *Sloanea*, *Hyeronima* and *Pourouma* are also prominent. The liana forests at El Chore are characterised by the abundance of *Combretum*, *Phenakospermum*, *Crepidospermum*, *Astronium*, *Talisia* as well as representatives of the Moraceae, Cecropiaceae and Ulmaceae families. The seasonally inundated plots at Las Londras are dominated by *Rinoreocarpus* as well as *Miconia*, *Inga*, *Xylopia, Guarea* and *Sloanea. Brosimum* and other Moraceae genera are also well-represented here. Riparian forest communities at Monte Cristo

are dominated by *Brosimum* and *Maquira* of the Moraceae family, as well as *Trichilia*, *Pouteria*, *Nectandra*, *Casearia* and genera of the Annonaceae family.

Table 3.5-1: Floristic composition (Relative Density) at the genus level of the most abundant woody plants (d.b.h. ≥ 10cm) growing within each of the studied rainforest communities.

Los Fierros 1	Rel. Density	Los Fierros 2	Rel. Density	El Chore 1	Rel. Density	El Chore 2	Rel. Density
Strelitziaceae *Phenakospermum*	12.76	Moraceae *Pseudolmedia*	11.14	Strelitziaceae *Phenakospermum*	29.00	Combretaceae *Combretum*	11.83
Moraceae *Pseudolmedia*	10.71	Arecaceae *Euterpe*	10.89	Bignoniaceae *Adenocalymma*	4.61	Sapindaceae *Talisia*	7.12
Arecaceae *Euterpe*	6.74	Strelitziaceae *Phenakospermum*	9.90	Moraceae *Pseudolmedia*	4.07	Anacardiaceae *Astronium*	4.19
Vochysiaceae *Qualea*	6.26	Melastomataceae *Miconia*	7.30	Burseraceae *Crepidospermum*	2.89	Burseraceae *Crepidospermum*	3.46
Rubiaceae *Capirona*	6.14	Elaeocarpaceae *Sloanea*	6.31	Combretaceae *Combretum*	2.62	Fabaceae *Erythrina*	3.46
Melastomataceae *Miconia*	4.69	Vochysiaceae *Qualea*	4.58	Fabaceae *Inga*	2.53	Lauraceae *Ocotea*	3.14
Vochysiaceae *Erisma*	4.09	Vochysiaceae *Erisma*	4.21	Hippocrateaceae *Cheiloclinium*	2.44	Elaeocarpaceae *Sloanea*	3.04
Elaeocarpaceae *Sloanea*	3.37	Rubiaceae *Capirona*	3.84	Anacardiaceae *Astronium*	2.17	Fabaceae *mimosa*	2.72
Melastomataceae	3.01	Euphorbiaceae *Hyeronima*	3.47	Lauraceae *Ocotea*	1.99	Bignoniaceae *Adenocalymma*	2.62
Rubiaceae *Amaioua*	3.01	Arecaceae *Socratea*	3.09	Annonaceae *Xylopia*	1.72	Fabaceae *Platypodium*	2.41
Hippocrateaceae *Cheiloclinium*	2.77	Melastomataceae	2.60	Melastomataceae *Miconia*	1.63	Fabaceae *Inga*	2.09
Euphorbiaceae *Hyeronima*	2.41	Moraceae *Brosimum*	2.35	Sapindaceae *Talisia*	1.54	Rutaceae *Metrodorea*	2.09
Arecaceae *Socratea*	2.05	Hippocrateaceae *Cheiloclinium*	2.35	Moraceae *Helicostylis*	1.45	Euphorbiaceae *Mabea*	1.99
Cecropiaceae *Pourouma*	1.81	Moraceae *Helicostylis*	2.10	Cecropiaceae *Pourouma*	1.45	Ulmaceae *Celtis*	1.68
Moraceae *Brosimum*	1.68	Rubiaceae *Amaioua*	1.73	Fabaceae *Pterocarpus*	1.45	Moraceae *Pseudolmedia*	1.57
Sapotaceae *Pouteria*	1.68	Cecropiaceae *Pourouma*	1.61	Elaeocarpaceae *Sloanea*	1.36	Sapindaceae *Serjania*	1.36
Apocynaceae *Aspidosperma*	1.32	Hippocrateaceae *Prionostemma*	1.49	Fabaceae *Platypodium*	1.17	Apocynaceae *Aspidosperma*	1.26
Annonaceae *Guatteria*	1.20	Vochysiaceae *Vochysia*	1.36	Hernandiaceae *Sparattanthelium*	1.17	Fabaceae *Machaerium*	1.26
Lauraceae *Nectandra*	1.20	Lauraceae	1.24	Cecropiaceae *Cecropia*	1.08	Bignoniaceae *Mussatia*	1.26

Table 3.5-1: *continued*

Las Londras 1	Rel. Density	Las Londras 2	Rel. Density	Monte Cristo 1	Rel. Density	Monte Cristo 2	Rel. Density
Violaceae *Rinoreocarpus*	13.44	Violaceae *Rinoreocarpus*	20.75	Annonaceae	15.23	Moraceae *Brosimum*	12.87
Fabaceae *Inga*	10.94	Melastomataceae *Miconia*	13.16	Moraceae *Brosimum*	13.67	Annonaceae	6.93
Sapotaceae *Pouteria*	6.67	Annonaceae *Xylopia*	5.77	Polygonaceae *Symmeria*	11.87	Fabaceae *Derris*	6.82
Melastomataceae *Miconia*	4.69	Arecaceae *Euterpe*	4.15	Meliaceae *Trichilia*	8.67	Sapotaceae *Pouteria*	5.50
Annonaceae *Xylopia*	4.27	Fabaceae *Derris*	3.64	Moraceae *Maquira*	8.15	Meliaceae *Trichilia*	5.06
Meliaceae *Guarea*	4.27	Fabaceae *Inga*	3.14	Sapotaceae *Pouteria*	5.40	Sapotaceae *Micropholis*	5.06
Rubiaceae *Uncaria*	3.23	Rubiaceae *Uncaria*	2.83	Fabaceae *Derris*	3.60	Fabaceae *Inga*	4.84
Elaeocarpaceae *Sloanea*	2.81	Vochysiaceae *Vochysia*	2.53	Melastomataceae *Mouriri*	3.25	Moraceae *Maquira*	4.40
Fabaceae *Derris*	2.60	Sapotaceae *Pouteria*	2.22	Sapotaceae *Micropholis*	2.76	Euphorbiaceae *Hevea*	4.07
Moraceae *Brosimum*	2.40	Hippocrateaceae *Cheiloclinium*	2.13	Lauraceae *Nectandra*	2.64	Flacourtiaceae *Casearia*	3.52
Moraceae *Sorocea*	1.98	Meliaceae *Guarea*	1.92	Ebenaceae *Diospyros*	2.64	Annonaceae *Xylopia*	3.41
Moraceae *Helicostylis*	1.98	Elaeocarpaceae *Sloanea*	1.82	Fabaceae *Inga*	2.40	Lauraceae *Nectandra*	3.08
Lauraceae *Nectandra*	1.67	Anacardiaceae *Tapirira*	1.62	Flacourtiaceae *Casearia*	2.16	Myristicaceae *Virola*	2.97
Arecaceae *Euterpe*	1.56	Chrysobalanaceae *Hirtella*	1.32	Chrysobalanaceae *Licania*	1.92	Chrysobalanaceae *Licania*	2.53
Annonaceae *Guatteria*	1.56	Moraceae *Pseudolmedia*	1.32	Cecropiaceae *Cecropia*	1.44	Fabaceae *Abarema*	1.76
Vochysiaceae *Vochysia*	1.46	Chrysobalanaceae *Licania*	1.32	Polygonaceae *Coccoloba*	1.44	Malpighiaceae *Banisteriopsis*	1.54
Chrysobalanaceae *Hirtella*	1.46	Bignoniaceae *Arrabidaea*	1.21	Moraceae *Pseudolmedia*	1.08	Fabaceae *Macrolobium*	1.54
Bignoniaceae *Arrabidaea*	1.35	Nyctaginaceae *Neea*	1.21	Fabaceae *Abarema*	0.96	Chrysobalanaceae *Hirtella*	1.54
Boraginaceae *Cordia*	1.25	Melastomataceae *Tibouchina*	1.21	Myrtaceae *Calyptranthes*	0.96	Meliaceae *Guarea*	1.43

3.5.2 *Pollen data*

Of the 78 pollen types identified within the pollen rain of NKMNP, most were identified to the family or generic taxonomic level. Unidentified taxa represented on average ca. 5% of the pollen sum. Mean pollen accumulation rates (PAR, grains cm^{-2} $year^{-1}$) across all rainforest sites was 6492 ± 3025 grains cm^{-2} $year^{-1}$; however, there was a significant difference between mean pollen accumulation rates in *terra firme* plots (Los Fierros, 10476 grains cm^{-2} $year^{-1}$; 95% CI: 8389 – 13391; El Chore, 7433 grains cm^{-2} $year^{-1}$; 95% CI: 5909 – 9374) and seasonally inundated and riparian forest plots (Las Londras, 5806 grains cm^{-2} $year^{-1}$ 95% CI: 4859 - 6941; Monte Cristo, 4401 grains cm^{-2} $year^{-1}$; 95% CI: 3754 - 5159). Indeed, between-site differences in the pollen accumulation rate reveal a gradient of pollen influx that exhibits high PAR values within *terra firme* forests and lower values in flooded forest communities (Fig. 3.5-1).

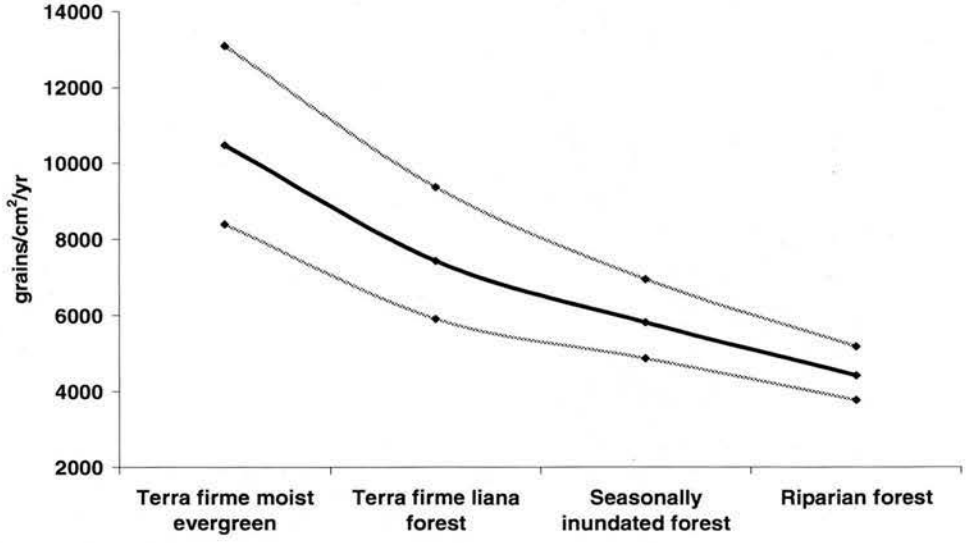

Fig. 3.5-1: Differences in Pollen Accumulation Rates (PAR) values (grains cm^{-2} $year^{-1}$) between each of the studied plant communities. Black line: mean PAR value; grey lines: 95% confidence limits on PAR calculations.

The percentage pollen diagram presented in Fig. 3.5-2 shows the most abundance pollen types found within the pollen rain of the four studied communities as well as in surface sediment samples obtained from the five studied lakes. Fig. 3.5-3 shows PAR values for selected taxa. Genera of the predominantly anemophilous Moraceae family include *Brosimum*, *Helicostylis*, *Pseudolmedia*, *Maquira* and *Sorocea* (See Burn and Mayle, in press) and are extremely well-represented in both pollen trap and surface sample spectra. When combined with pollen of the Urticalean rosids Cecropiceae and Urticaceae, the average abundance of these families makes up 48% of the total pollen sum, 53% in *terra firme* rainforest communities and 45% in seasonally inundated and riparian communities. The disturbance indicators *Cecropia*, *Pourouma* and Melastomataceae/Combretaceae are abundant within the pollen rain as well as *Celtis* and *Trema*, two wind-pollinated genera of the Ulmaceae family. Arecaceae, *Alchornea*, *Didymopanax*, *Sloanea* and *Banisteriopsis* are ubiquitous and exhibit relatively low abundance values across the plots. However, *Didymopanax* and Arecaceae pollen is more abundant in liana forests and *Alchornea* pollen displays increased abundance in riparian forest communities. Ecosystem-specific indicator taxa include *Tapirira* and *Hyeronima*, which are only present in pollen rain sampled from *terra firme* evergreen forest at Los Fierros. *Pouteria*, *Sapium* and *Symmeria* are restricted to riparian forests at Monte Cristo, and *Cordia* pollen is only found in liana forests at El Chore. The importance of these taxa is clear on examination of the PAR diagram (Fig. 3.5-3).

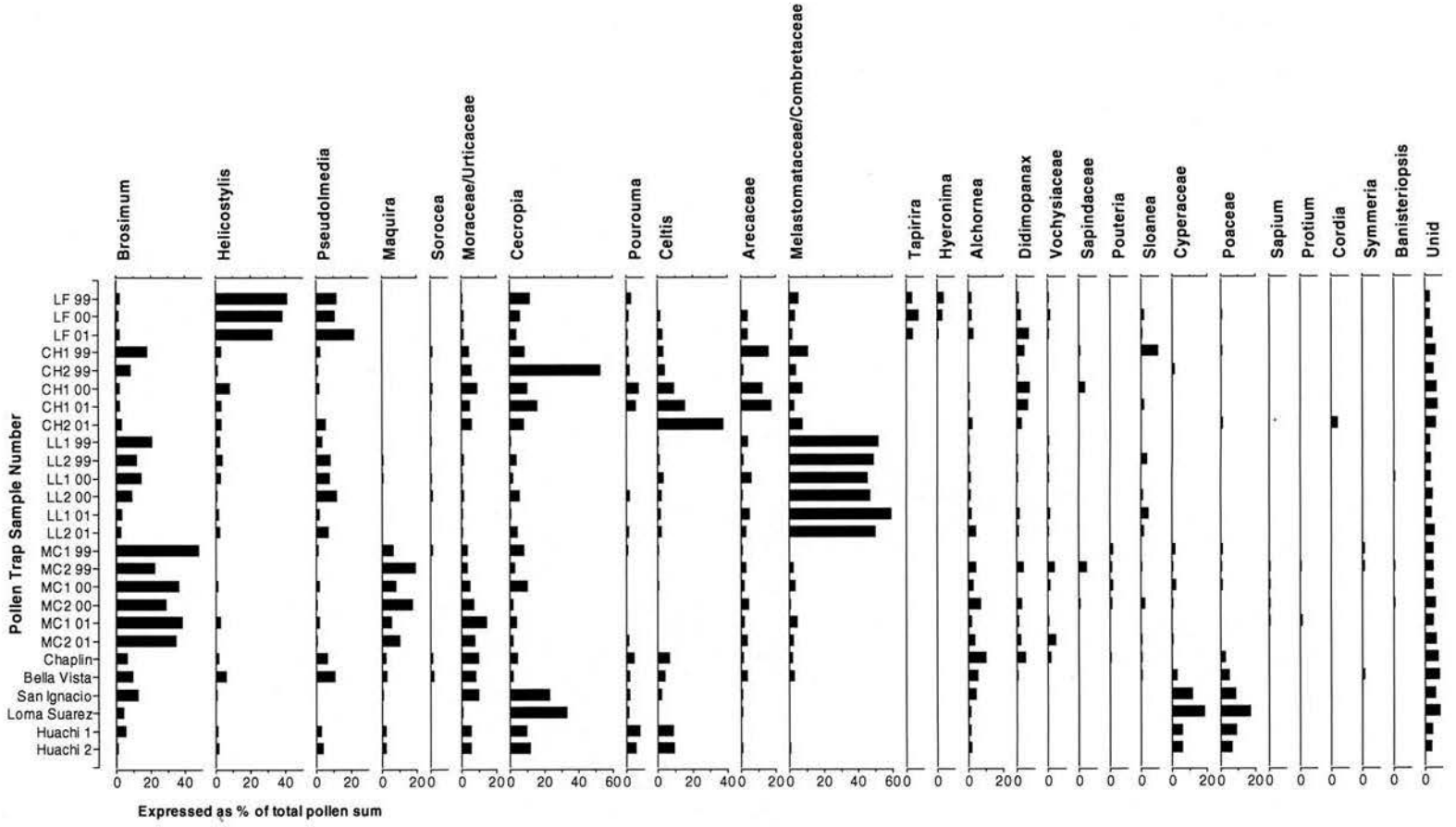

Fig. 3.5-2: Pollen percentage diagram showing the most common of the 78 identifiable pollen taxa identified in both trap and lake surface samples (Lowermost six samples). LF, Los Fierros (Terra firme moist evergreen rainforest); CH, El Chore (terra firme liana forest); LL, Las Londras (Seasonally inundated rainforest); MC, Monte Cristo (Riparian rainforest).

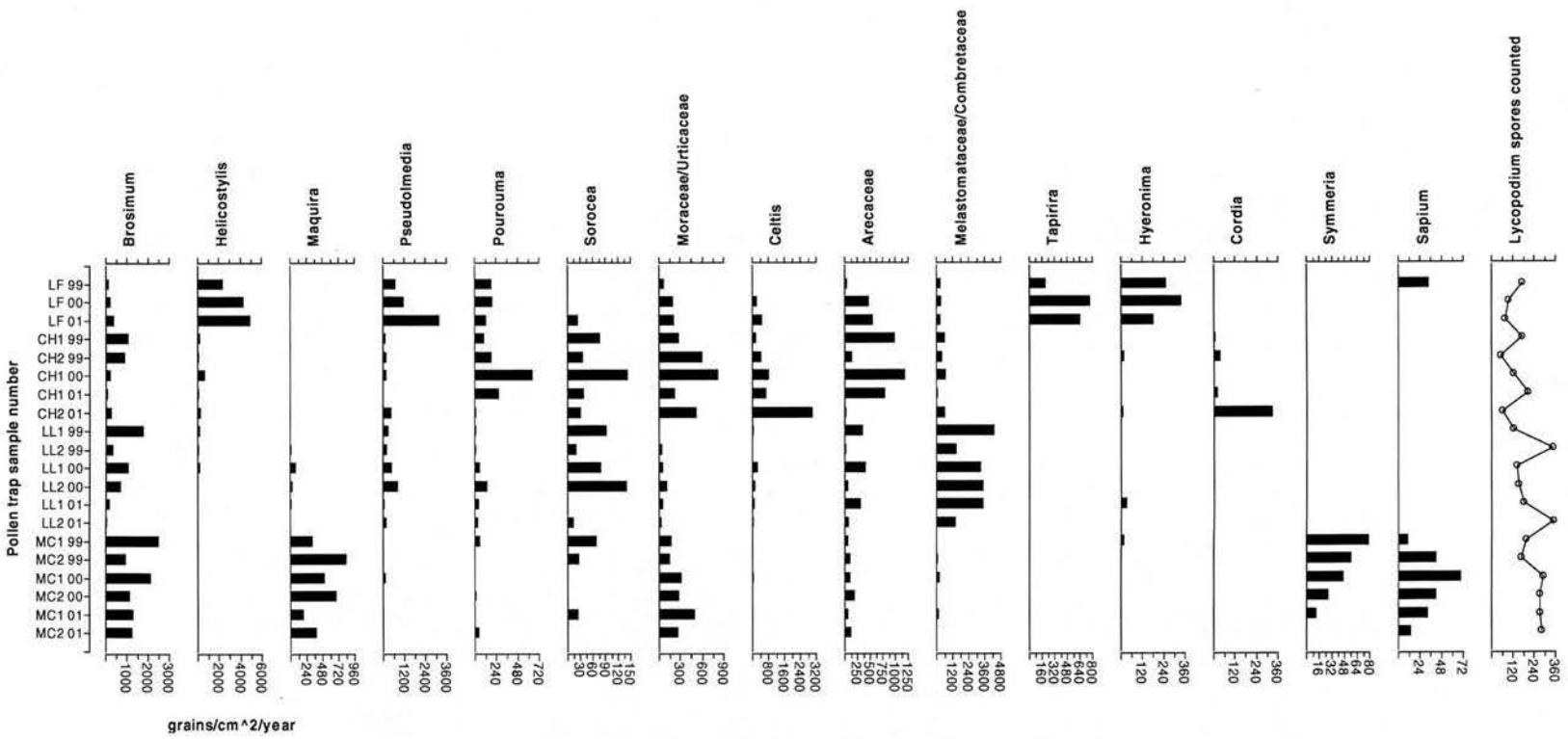

Fig. 3.5-3: Pollen accumulation rate (PAR) diagram for selected taxa identified within the pollen trap samples. LF, Los Fierros (Terra firme moist evergreen rainforest); CH, El Chore (terra firme liana forest); LL, Las Londras (Seasonally inundated rainforest); MC, Monte Cristo (Riparian rainforest).

Of the Moraceae family, *Brosimum* pollen is present at all sites and represents a considerable proportion of the pollen sum in trap and surface sediment samples. It is at its most abundant in riparian forest communities at Monte Cristo comprising ca. 40% of the total pollen sum. *Helicostylis* pollen dominates pollen spectra at Los Fierros where it makes up 30-40% of the total pollen sum but remains below 10% at all other sites. *Pseudolmedia* pollen makes up ca. 10% of the pollen sum at Los Fierros and Las Londras as well as in the surface samples at Laguna Bella Vista and Laguna Chaplin. *Maquira* pollen is restricted to seasonally inundated and riparian forests making up ca. 15% of the pollen rain within the latter. The disturbance indicators *Pourouma* and *Cecropia* are particularly prominant in the *terra firme* plots but also constitute a significant proportion (20 – 40%) of the surface sediment samples at San Ignacio de Moxos and Loma Suarez situated within rain forests of the Llanos de Moxos ecoregion (Beni Basin).

Celtis is well-represented within pollen spectra of liana forest sites at El Chore and comprises up to 10% of the surface sediment spectra at Laguna Chaplin, Laguna Bella Vista and Laguna Huachi. *Trema* pollen is not well-represented within the Noel Kempff Mercado National Park, but it dominates the sediment samples at Laguna Huachi, comprising ca. 20% of the pollen sum. Grasses and sedges (Poaceae and Cyperaceae) represent a relatively small component of the trap and sediment samples within NKMNP; however, they are abundant in the gallery forest sites Laguna Loma Suarez and San Ignacio de Moxos making up 10 – 20% of the total pollen sum. At Laguna Huachi, Laguna Bella Vista and Laguna Chaplin, the abundance of Poaceae and Cyperaceae is only slightly higher than in the trap samples.

3.5.3 *Ordination and classification of floristic data*

The results of PCA ordination and UPGMA cluster analysis on the covariance data matrix of the floristic inventories are presented in Fig. 3.5-4. PCA on the covariance data matrix produces a clear ordination of plots based on their species composition (Fig. 3.5-4 (a)). The ordination reveals seven orthogonal principal components of which the first ($\lambda_1 = 16.34$) and second ($\lambda_2 = 9.67$) explain 64% of the variance within the dataset. Fig. 3.5-4 (b) illustrates the relative influence of species on the first two principal components. The first principal component separates *terra firme* rainforests to the left of the graph from seasonally-inundated and riparian forests to the right (Fig. 3.5-4 (a)). The upper left quadrant of the ordination diagram is strongly influenced by the abundance of *Phenakospermum*, *Pseudolmedia*, *Hyeronima* and *Pourouma* (Fig. 3.5-4 (b)) and comprises three of the *terra firme* plots (Fig. 3.5-4 (a)). *Phenakospermum* is not recorded within the floristic inventories at El Chore-2, which explains the separation of this site from the other *terra firme* plots. The seasonally inundated plots, Las Londras 1 and 2, occupy the lower end of the second principal component and are influenced by the abundance of *Rinoreocarpus* (Violaceae), *Inga*, *Guarea*, *Sorocea* and Melastomataceae/Combretaceae. Riparian plots occupy the upper right quadrant of the ordination diagram, their position being driven by the abundance of *Brosimum*, *Maquira*, *Symmeria*, Trichilia, *Casearea* and the Annonaceae family. The separation of forest communities by means of PCA on the covariance matrix is supported by the results of average-linkage UPGMA cluster analysis, which divides the plots into four main clusters according to their floristic similarity (Fig. 3.5-4 (c)). The resulting dendrogram shows that different plots sampled from within the same forest

community exhibit a consistent floristic composition with the exception of plots at El Chore where the absence of *Phenakospermum* prevents fusion of sites into one group. Cluster analysis also demonstrates a clear separation of inundated and riparian forests that occupy the left half of the dendrogram and *terra firme* forest that occupy the right half.

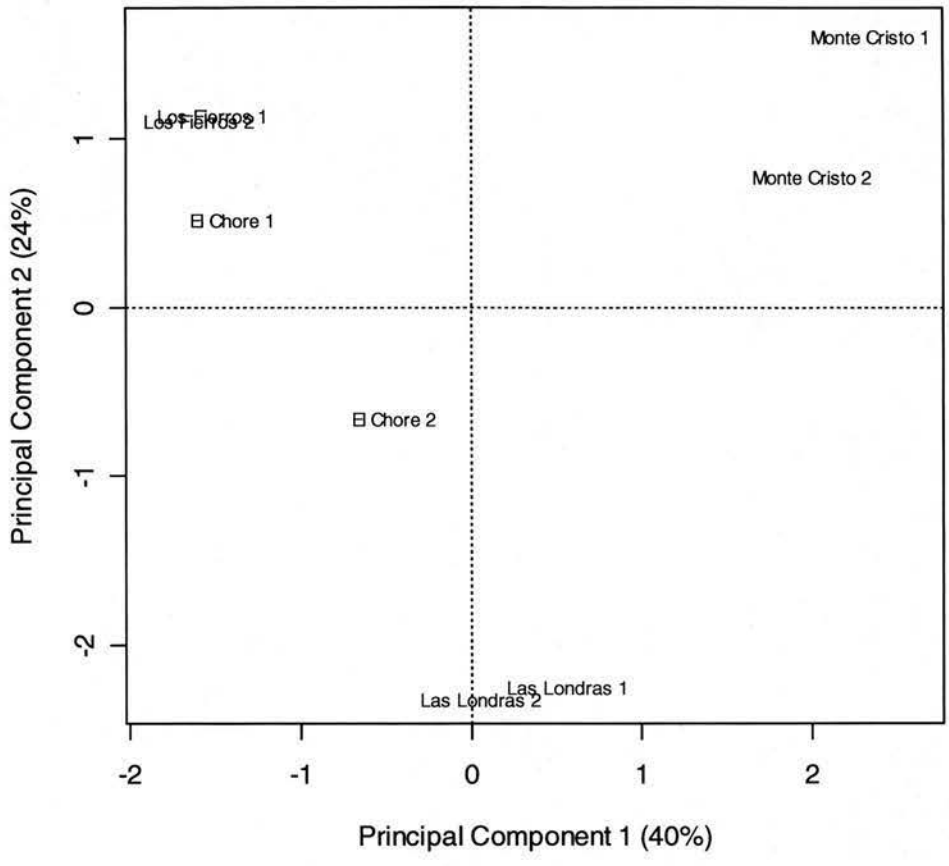

Fig. 3.5-4: a) Quadrat ordination of floristic data obtained from four plant communities within NKMNP using Principal Components Analysis (PCA). Monte Cristo 1 and 2 (Riparian forest plots), Las Londras 1 and 2 (seasonally inundated raiforest plots), El Chore (*terra firme* liana rainforests plots), Los Fierros 1 and 2 (*terra firme* moist evergreen rainforest plots).

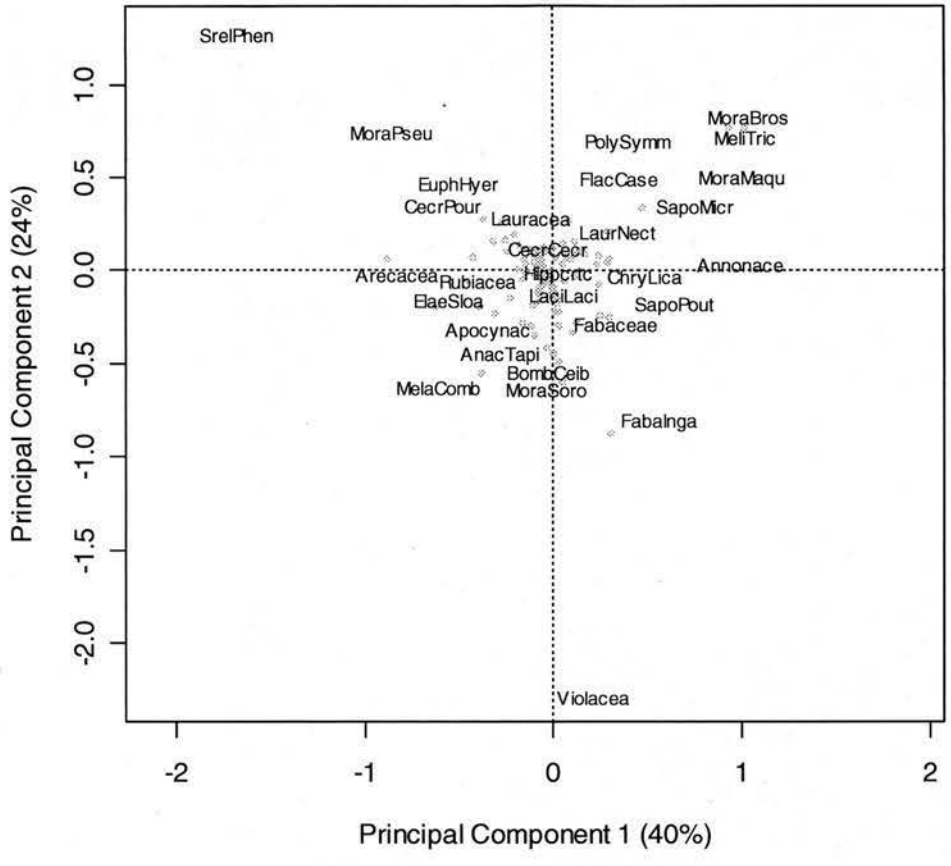

Fig. 3.5-4: b) PCA species ordination of the floristic data. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

SrelPhen	Strelitziaceae *Phenakospermum*	ChryLica	Chrysobalanceae *Licania*
MoraPseu	Moraceae *Pseudolmedia*	Rubiacea	Rubiaceae
MoraBros	Moraceae *Brosimum*	LaciLaci	Lacismataceae *Lacisma*
PolySymm	Polygonaceae *Symmeria*	ElaeSloa	Elaeocarpaceae *Sloanea*
MeliTric	Meliaceae *Trichilia*	SapoPout	Sapotaceae *Pouteria*
FlacCase	Flacourtaceae *Casearia*	Apocynac	Apocynaceae
MoraMaqu	Moraceae *Maquira*	Fabaceae	Fabaceae
EuphHyer	Euphorbiaceae *Hyeronima*	AnacTapi	Anacardiaceae *Tapirira*
CecrPour	Cecropiaceae *Pourouma*	BombCeib	Bombacaceae *Ceiba*
SapoMicr	Sapotaceae *Micropholis*	MelaComb	Melastomataceae/ Combretaceae
Lauracea	Lauraceae		
LaurNect	Lauraceae *Nectandra*	MoraSoro	Moraceae *Sorocea*
CecrCecr	Ceacropiaceae *Cecropia*	FabaInga	Fabaceae *Inga*
Annonace	Annonaceae	Violacea	Violaceae
Arecacea	Arecaceae		
Hippcrtc	Hippocrataceae		

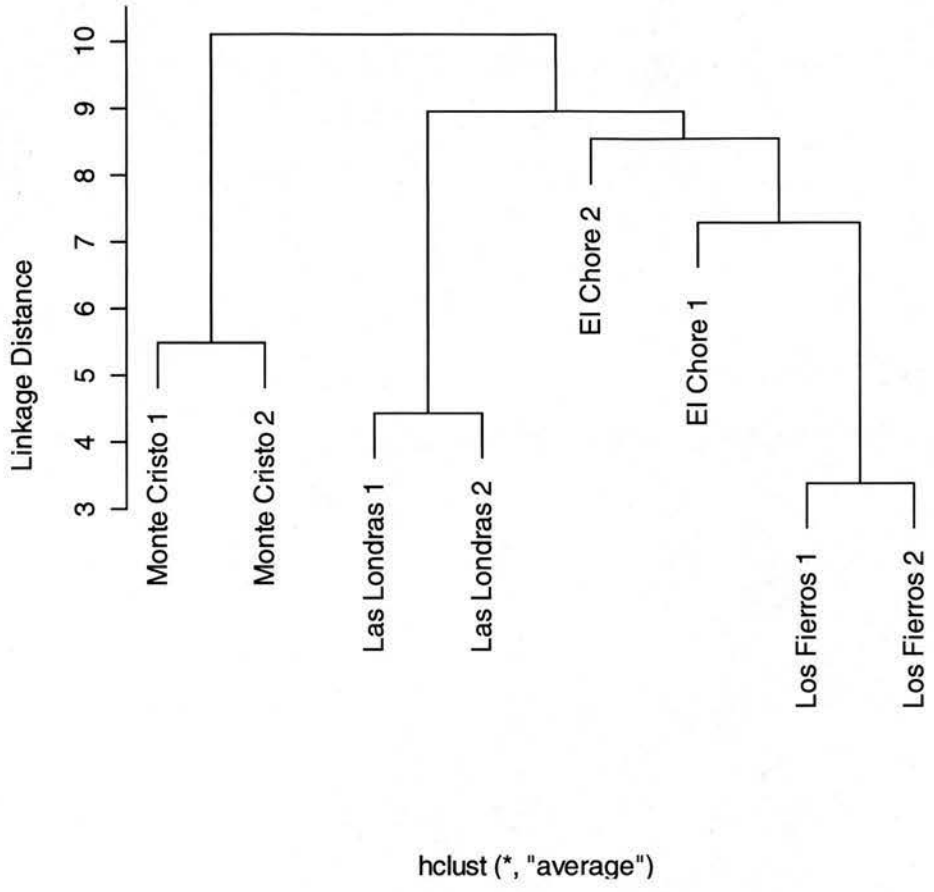

Fig. 3.5-4: c) Cluster analysis of floristic data using the Unweighted Pair Group with Arithmetic Mean (UPGMA) classification technique. Monte Cristo 1 and 2 (Riparian forest plots), Las Londras 1 and 2 (seasonally inundated raiforest plots), El Chore (*terra firme* liana rainforests plots), Los Fierros 1 and 2 (*terra firme* moist evergreen rainforest plots).

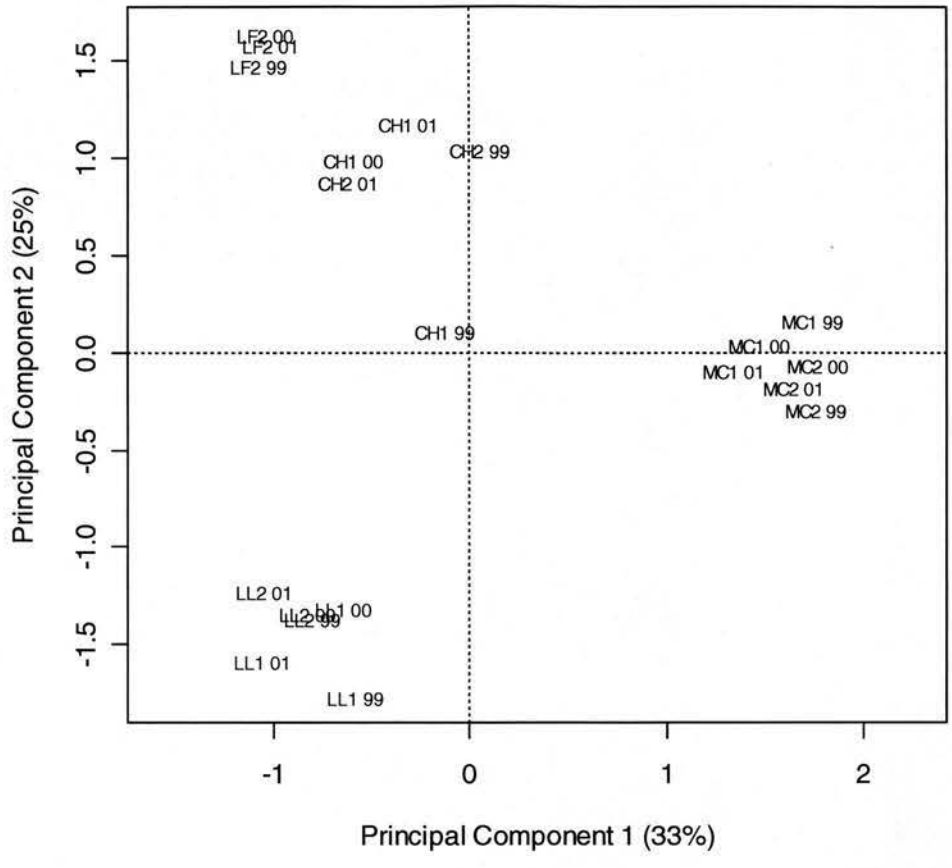

Fig. 3.5-4: d) Quadrat ordination of pollen data obtained from four plant communities within NKMNP using Principal Components Analysis (PCA). MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros). 99 = 1999; 00 = 2000; 01 = 2001.

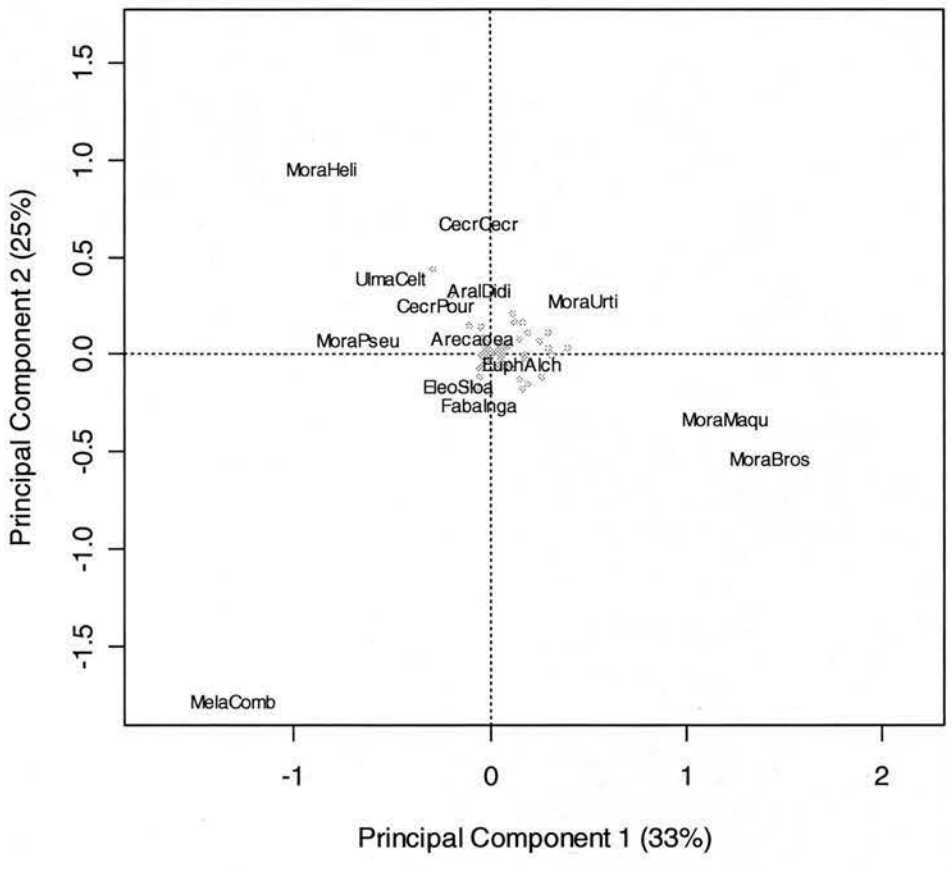

Fig. 3.5-4: e) Taxon ordination (PCA) of the pollen trap data. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

MoraHeli	Moraceae *Helicostylis*
CecrCecr	Cecropiaceae *Cecropia*
UlmaCelt	Ulmaceae *Celtis*
AralDidi	Araliaceae *Didimopanax*
Mora/Urti	Moraceae/Urticaceae
MoraPseu	Moraceae *Pseudolmedia*
Arecacea	Arecaceae
EuphAlch	Euphorbiaceae *Alchornea*
ElaeSloa	Elaeocarpaceae *Sloanea*
FabaInga	Fabaceae *Inga*
MoraMaqu	Moraceae *Maquira*
MoraBros	Moraceae *Brosimum*
MelaComb	Melastomataceae/Combretaceae

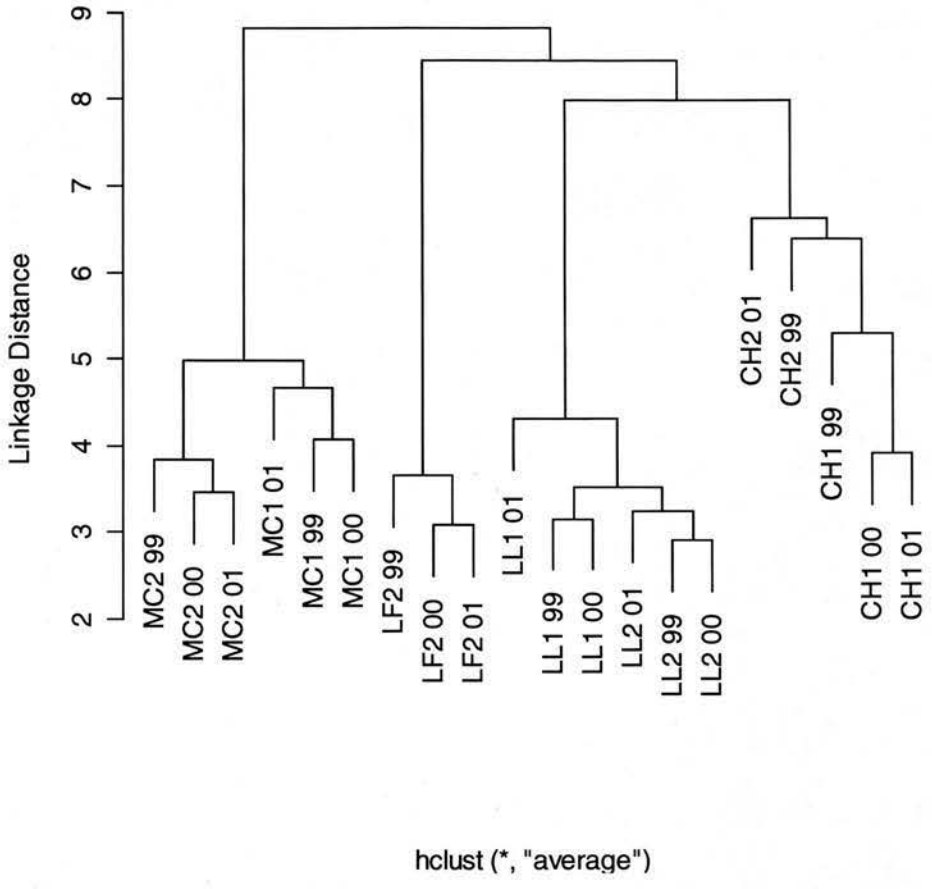

Fig. 3.5-4: f) Cluster analysis of pollen trap data using the UPGMA classification technique. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros). 99 = 1999; 00 = 2000; 01 = 2001.

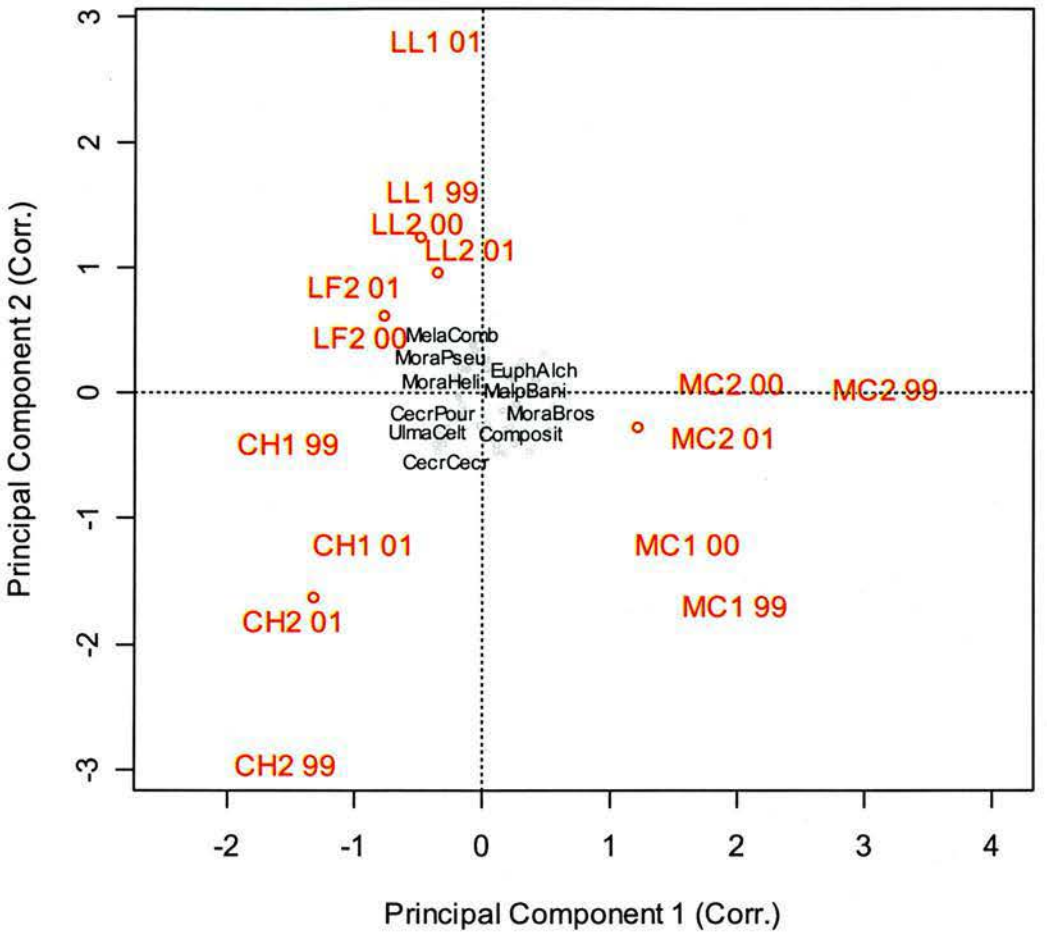

Fig. 3.5-5: a) Quadrat ordination of pollen trap data obtained from four plant communities within NKMNP using Principal Components Analysis (PCA) on the correlation matrix. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros). 99 = 1999; 00 = 2000; 01 = 2001. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

MelaComb	Melastomataceae/Combretaceae
MoraPseu	Moraceae Pseudolmedia
EuphAlch	Euphorbiaceae Alchornea
MoraHeli	Moraceae Helicostylis
MalpBani	Malpighiaceae Banisteriopsis
MoraBros	Moraceae Brosimum
CecrPour	Cecropiaceae Pourouma
UlmaCelt	Ulmaceae Celtis
Composit	Compositae (Asteraceae)
CecrCecr	Cecropiaceae Cecropia

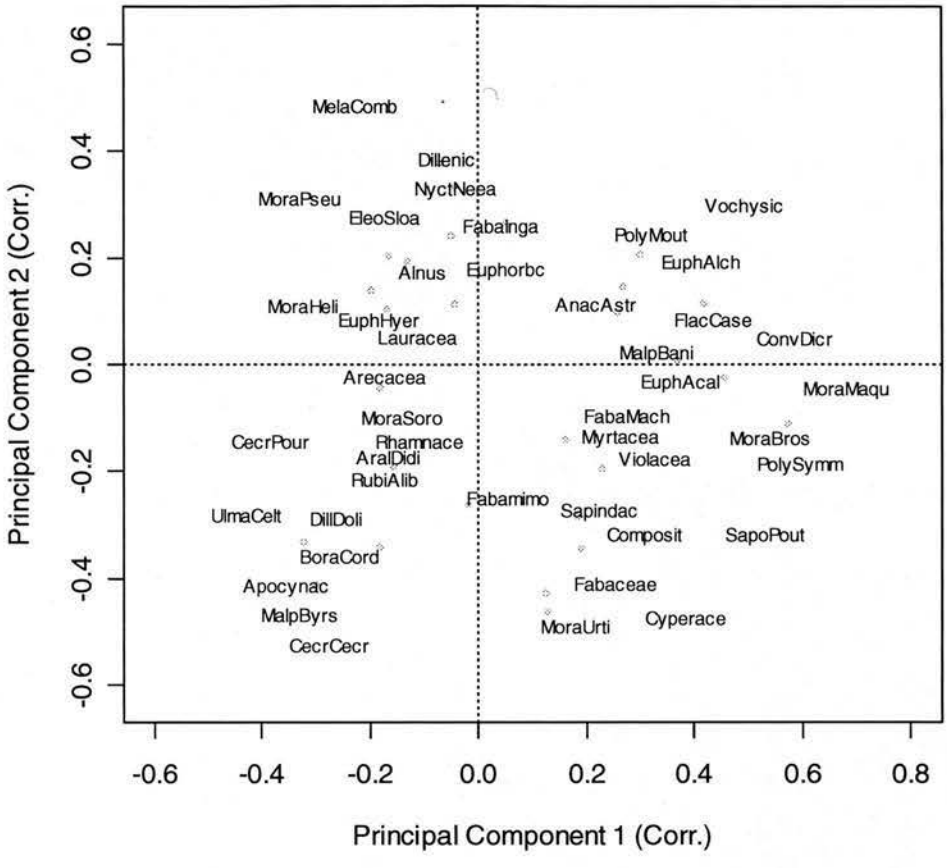

Fig. 3.5-5: b) Taxon ordination (PCA) on the correlation matrix of the pollen trap data. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

MelaComb	Melastomataceae/ Combretaceae	ConvDIcr	Convolvulaceae *Dicranostyles*
Dillenic	Dilleniaceae	MalpBani	Malpighiaceae *Banisteriopsis*
NyctNeea	Nyctaginaceae *Neea*	Arecacea	Arecaceae
Mora Pseu	Moraceae *Pseudolmedia*	EuphAlch	Euphorbiaceae *Alchornea*
EleoSloa	Elaeocarpaceae *Sloanea*	MoraMaqu	Moraceae *Maquira*
FabaInga	Fabaceae *Inga*	MoraSoro	Moraceae *Sorocea*
Vochysic	Vochysiaceae	FabaMach	Fabaceae *Machaerium*
PolyMout	Polygalaceae *Moutabia*	CecrPour	Cecropiaceae *Pourouma*
EuphAlch	Euphorbiaceae *Alchornea*	Rhamnace	Rhamnaceae
Euphorbsc	Euphorbiaceae	Myrtacea	Myrtaceae
Alnus	Betulaceae *Alnus*	MoraBros	Moraceae *Brosimum*
MoraHeli	Moraceae *Helicostylis*	AralDidi	Araliaceae *Didimopanax*
AnacAstr	Anacardiaceae *Astronium*	Violacea	Violaceae
EuphHyer	Euphorbiaceae *Hyeronima*	PolySymm	Polygonaceae *Symmeria*
FlacCase	Flacourtiaceae *Casearia*	RubiAlib	Rubiaceae *Alibertia*
Lauracea	Lauraceae	Fabamimo	Fabaceae *mimosa*
UlmaCelt	Ulmaceae *Celtis*	Sapindac	Sapindaceae
Composit	Compositae (Asteraceae)	DillDoli	Dilleniaceae *Doliocarpus*
BoraCord	Boraginaceae *Cordia*	SapoPout	Sapotaceae *Pouteria*
MalpByrs	Malpighiaceae *Byrsonima*	Apocyn	Apocynaceae
Cyperace	Cyperaceae	MoraUrti	Moraceae/Urticaceae
		CecrCecr	Cecropiaceae *Cecropia*

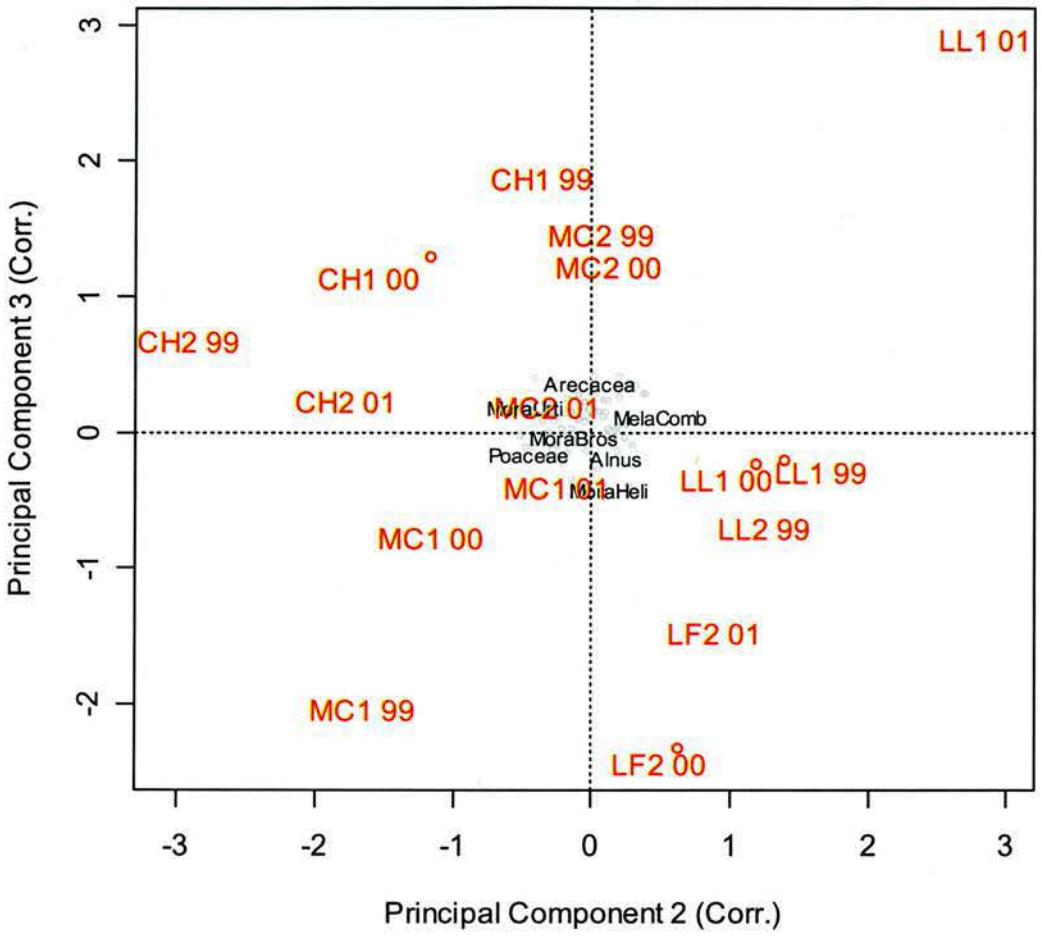

Fig. 3.5-5: c) Sample ordination (PCA) showing the second and third principal components. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros). 99 = 1999; 00 = 2000; 01 = 2001. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

Areacea	Arecaceae
MoraUrti	Moraceae/Urticaceae
MelaComb	Melastomataceae/Combretaceae
MoraBros	Moraceae *Brosimum*
Poaceae	Poaceae
Alnus	Betulaceae *Alnus*
MoraHeli	Moraceae *Helicostylis*

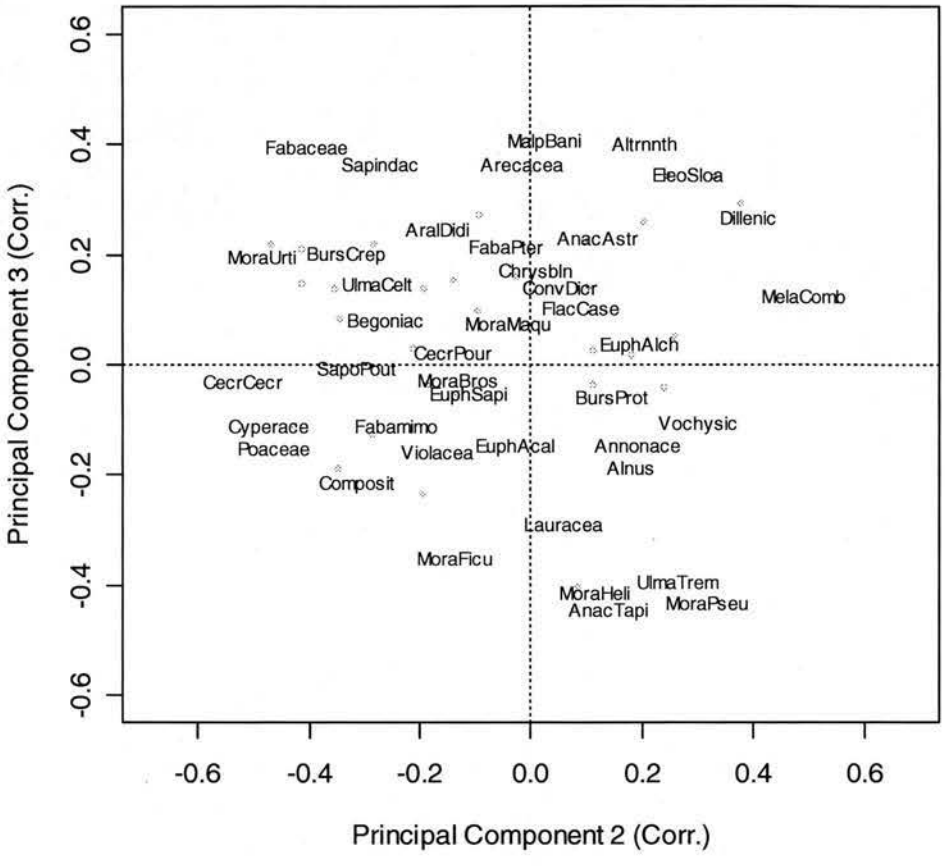

Fig. 3.5-5: d) Taxon ordination of pollen data obtained from four plant communities within NKMNP showing the second and third principal components. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity.

Key to represented taxa:

MalpBani	Malpighiaceae *Banisteriopsis*	MoraBros	Moraceae *Brosimum*
Alternnth	Amaranthaceae *Alternanthera*	EuphSapi	Euphorbiaceae *Sapium*
Sapindac	Sapindaceae	BursProt	Burseraceae *Protium*
Arecacea	Arecaceae	Cyperace	Cyperaceae
EleoSloa	Elaeocarpaceae *Sloanea*	Fabamimo	Fabaceae *Mimosa*
Dillenic	Dilleniaceae	Vochysic	Vochysiaceae
AralDidi	Araliaceae *Didimopanax*	EuphAcal	Euphorbiaceae *Acalypha*
AnacAstr	Anacardiaceae *Astronium*	Annonace	Annonaceae
FabaPter	Fabaceae *Pterocarpus*	Poaceae	Poaceae
BursCrep	Burseraceae *Crepidospermum*	Violacea	Violaceae
MoraUrti	Moraceae/Urticaceae	Alnus	Betulaceae *Alnus*
ChrysbIn	Chrysobalanceae	Composit	Compositae
UlmaCelt	Ulmaceae *Celtis*	Lauracea	Lauraceae
ConvDicr	Convolvulaceae *Dicranostyles*	MoraFicu	Moraceae *Ficus*
MelaComb	Melastomataceae/Combretaceae	UlmaTrem	Ulmaceae *Trema*
FlacCase	Flacourtaceae *Casearea*	MoraHeli	Moraceae *Helicostylis*
Begoniac	Begoniaceae	MoraPseu	Moraceae *Pseudolmedia*
MoraMaqu	Moraceae *Maquira*	AnacTapi	Anacardiaceae *Tapirira*
EuphAlch	Euphorbiaceae *Alchornea*		
CecrPour	Cecropiaceae *Pourouma*		
SapoPout	Sapotaceae *Pouteria*		
CecrCecr	Cecropiaceae *Cecropia*		

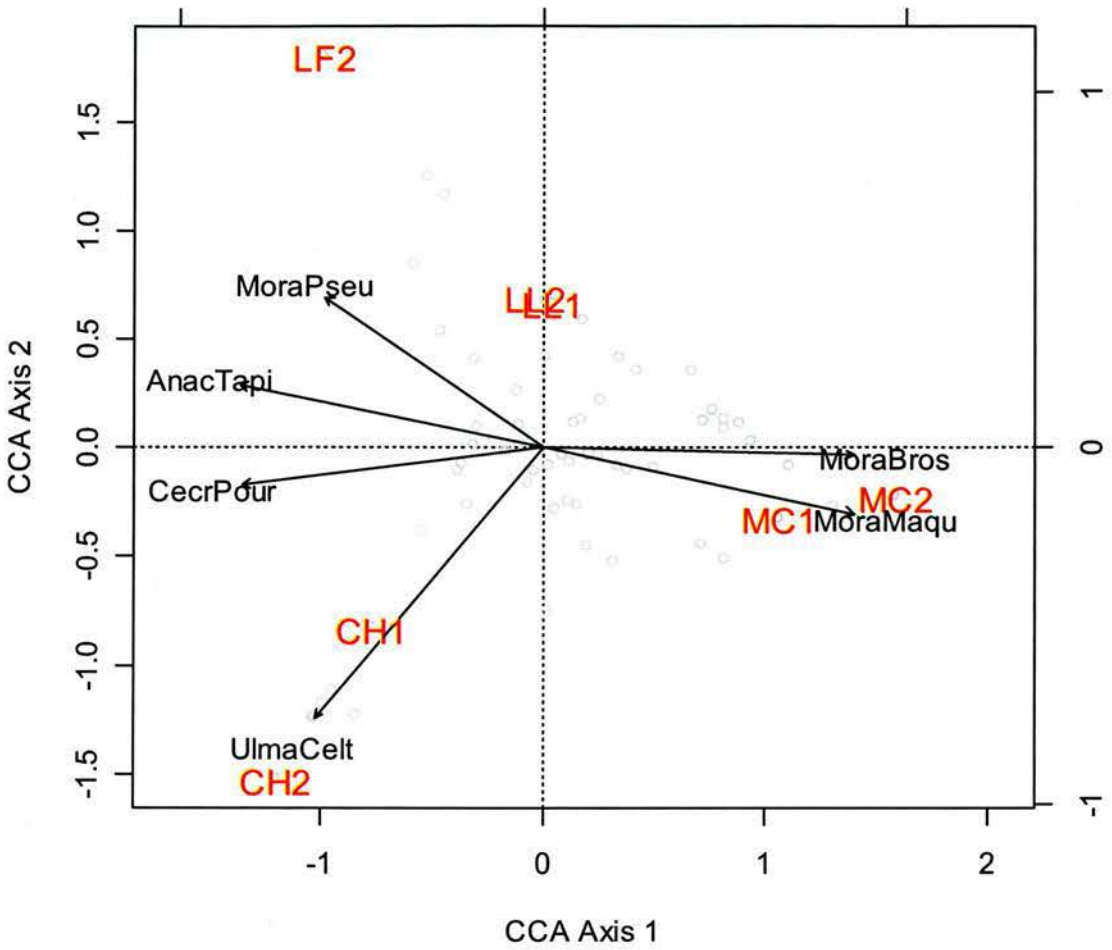

Fig. 3.5-5: e) Canonical correspondence analysis (CCA) of both floristic and pollen trap datasets from all four study plots. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraPseu	Moraceae *Pseudolmedia*
AnacTapi	Anacardiaceae *Tapirira*
CecrPour	Cecropiaceae *Pourouma*
MoraBros	Moraceae *Brosimum*
MoraMaqu	Moraceae *Maquira*
UlmaCelt	Ulmaceae *Celtis*

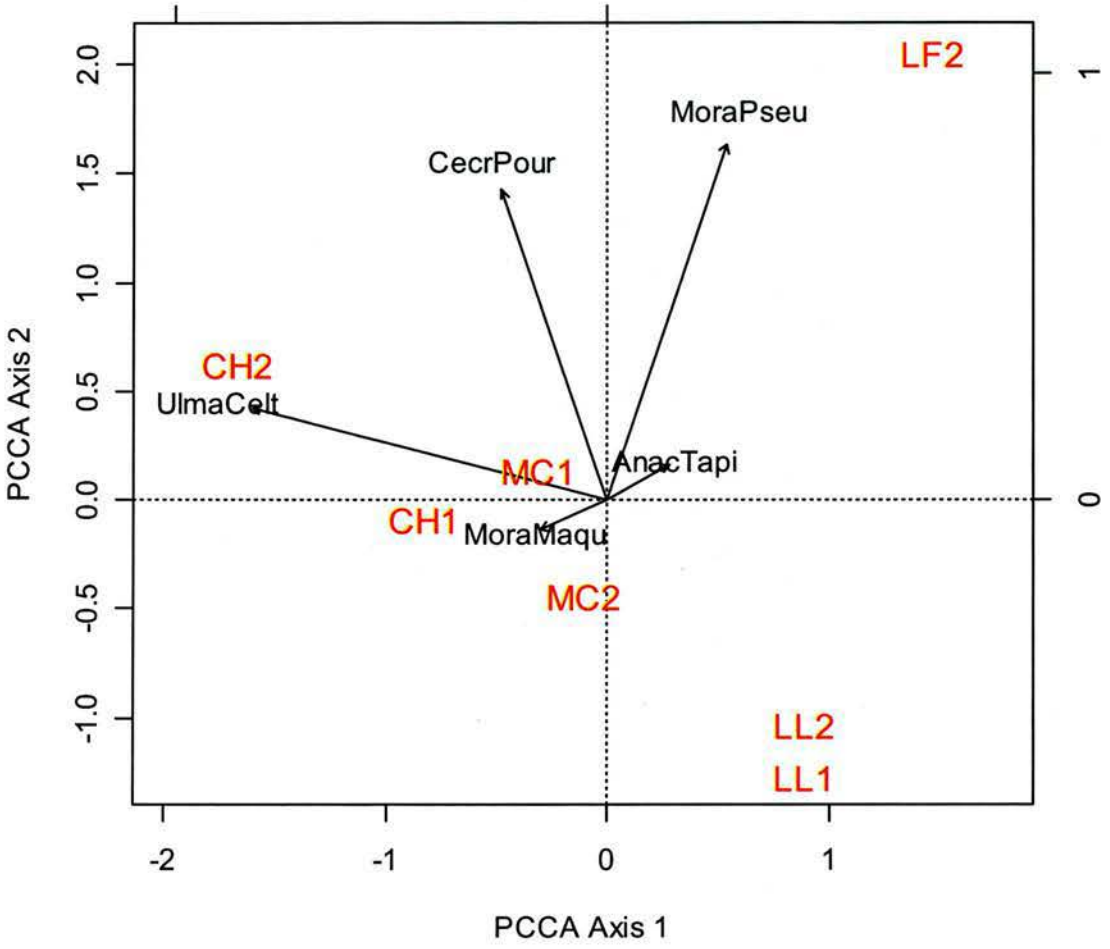

Fig. 3.5-5: f) Partial Canonical correspondence analysis after the removal of *Brosimum* pollen type. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraPseu	Moraceae *Pseudolmedia*
AnacTapi	Anacardiaceae *Tapirira*
CecrPour	Cecropiaceae *Pourouma*
MoraMaqu	Moraceae *Maquira*
UlmaCelt	Ulmaceae *Celtis*

3.5.4 *Ordination and classification of pollen data*

3.5.4.1 Indirect Ordination

PCA ordination on the covariance data matrix of the annual pollen trap samples reveals a separation of plots similar to that exhibited by the floristic data (Fig. 3.5-4 (d)) However, a comparison of the ordination diagrams of vegetation and pollen data matrices reveals that the distribution of sites is not, in all instances, driven by the same taxa (Fig. 3.5-4 (e)). Eigenvalues representing the first and second principal components ($\lambda_1 = 10.37$; $\lambda_2 = 7.87$) explain 59% of the variance within the pollen data matrix. The upper left quadrant of the ordination diagram is occupied by *terra firme* plant communities, the separation of which is driven by the abundance of the following pollen types: *Pseudolmedia*, *Cecropia*, *Pourouma*, *Helicostylis* and *Celtis* (Fig. 3.5-4 (e)). Furthermore, both *terra firme* communities may be differentiated from each other principally by the abundance of *Helicostylis* pollen at Los Fierros (tall moist evergreen forest) and *Celtis* pollen at El Chore (liana evergreen forest). Seasonally-inundated forests cluster in the lower left quadrant of the ordination diagram and are driven by the abundance of Melastomataceae/Combretaceae pollen, which dominates the pollen spectra within these forests. *Maquira* and *Brosimum* drive the differentiation of riparian forest sites at Monte Cristo and occupy the upper end of the first principal component. In general, the inter-annual variability exhibited by pollen spectra sampled from the studied forests is low and confirmed by the spatial integrity of clusters in the ordination diagram (Fig. 3.5-4 (d)). The separation of trap CH1 99 can be explained by the atypical abundance of *Brosimum* at this site, which, in terms of similarity, draws it closer to the inundated and riparian forest communities. UPGMA cluster analysis confirms the palynological separation of

plant communities into four distinct groups based on their taxonomic (dis)similarity (Fig. 3.5-4 (f)). It should be noted that, in contrast to the floristic data, fusion does occur between plots at El Chore because *Phenakospermum* is not represented within the pollen rain.

PCA ordination of the correlation data matrix of annual pollen rain enables the detection of less abundant pollen taxa that help drive the differentiation of plots. However, once data is standardized to unit variance, the effect of dominant taxa on the distribution of plots, and as a consequence the integrity of individual clusters, is reduced (Fig. 3.5-5 (a-d)). Nevertheless, distinct groupings are still visible and the relative importance of less abundant taxa on the distribution of plots can be investigated. Figs. 3.5-5 (b and d) show all pollen taxa standardized to unit variance and when viewed in combination with the distribution of plots illustrated in Fig. 3.5-5 (a and c), suggests that the separation of liana plots at El Chore is driven by less-abundant taxa including *Cordia*, *Cecropia*, *Doliocarpus*, *Didymopanax*, Apocynaceae and Rubiaceae. Taxa driving the separation of riparian forest plots at Monte Cristo include *Symmeria*, *Dicranostyles*, *Casearia*, *Banisteriopsis*, *Pouteria*, *Alchornea*, Myrtaceae and Vochysiaceae. In contrast, taxa including *Sloanea*, Dilleniaceae, *Inga*, *Neea*, *Alternanthera* and Dilleniaceae characterise seasonally inundated plots at Las Londras and *Tapirira* and *Hyeronima* those at Los Fierros.

3.5.4.2 Direct Ordination

The constrained CCA performed on both vegetation and pollen data matrices produced eigenvalues ($\lambda_1 = 0.21$; $\lambda_2 = 0.16$; $\lambda_3 = 0.14$) that explain 82% of the variance in the pollen percentage data. The six most significant genera that explained this variation were *Brosimum* ($p<0.05$; Monte Carlo permutation test), *Maquira* (p<

0.05), *Celtis* ($p < 0.05$), *Pourouma* ($p < 0.05$), *Tapirira* ($p < 0.05$), and *Pseudolmedia* ($p < 0.1$; Fig. 3.5-5 (e)). The effect of removing any of these taxa from the analysis is demonstrated by the application of a partial CCA on both datasets. Fig. 3.5-5 (f) illustrates the effect of the removal of *Brosimum* from the analysis. Once removed, the remaining genera constraining the pollen data can only produce eigenvalues ($\lambda_1 = 0.15$; $\lambda_2 = 0.15$) that explain 48% of the total variance in the pollen percentage data. When *Brosimum* is included in the analysis the first two axes produce eigenvalues ($\lambda_1 = 0.21$; $\lambda_2 = 0.16$) that explain 58.3% of the variance.

3.5.5 *Ordination and classification of pollen trap and lake surface samples*

The results of PCA ordination on the covariance matrix of both pollen trap and surface sediment pollen spectra are presented in Fig. 3.5-6 alongside UPMGA cluster analysis (Figs. 3.5-6 (c and f)). The first three principal components ($\lambda_1 = 8.4$; $\lambda_2 = 7.2$; $\lambda_3 = 4.3$) explain 77% of the variance within the dataset. Surface samples at Laguna Bella Vista and Laguna Chaplin within NKMNP are comparable with rainforest pollen spectra obtained from pollen traps in terms of their taxonomic composition. The ordination diagram of the first two principal components reveals they occupy the upper right quadrant of the ordination diagram, midway between liana forest sites at El Chore and riparian forest communities at Monte Cristo, which suggests they contain both *terra firme* and riparian forest elements (Fig. 3.5-6 (a)). Observation of the second and third principal components demonstrates that pollen spectra within the surface sediments are most similar to riparian forests (Fig. 3.5-6 (b)). UPGMA Cluster analysis confirms this and suggests riparian forest communities at Monte Cristo represent the closest modern analogue for surface

samples obtained from lakes within NKMNP (Fig. 3.5-6 (c)). Importantly, these results are consistent with the modern day distribution of rainforest communities surrounding these lakes, confirmed by Landsat imagery of the sites presented in Fig. 3.3-1.

PCA ordination on the covariance matrix of pollen trap and surface sediment data obtained from the five studied lakes reveals a distinct division along the first principal component axis between pollen spectra obtained within NKMNP and those from elsewhere (Fig. 3.5-6 (d)). The first principal component ($\lambda_1 = 10.48$) accounts for 34.1% of the variance within the dataset and represents a gradient separating rainforest communities at NKMNP to the left of the ordination diagram from forest communities of the Beni Basin and *terra firme* forest communities at Laguna Huachi to the right. The abundance of Poaceae, Cyperaceae and *Cecropia* at Laguna Loma Suarez and San Ignacio de Moxos (Fig. 3.5-6 (d)), and of *Trema* at Laguna Huachi (Fig. 3.5-6 (e)) is instrumental in the separation of these sites from those within NKMNP. Cluster analysis confirms the dissimilarity between pollen spectra from NKMNP and those from Laguna Huachi and lakes in the Llanos de Moxos ecoregion (Fig. 3.5-6 (f)). Examination of the second principal component ($\lambda_2 = 5.79$), which explains a significant 18.9% of the variance in the data matrix shows that surface samples obtained from *terra firme* rainforest communities at Laguna Huachi are indeed similar to pollen spectra obtained from Los Fierros and El Chore at NKMNP. The third principal component ($\lambda_3 = 4.28$), which explains 14% of the variance indicates an association between pollen spectra of gallery forest lakes situated within the Llanos de Moxos and *terra firme* forests in NKMNP.

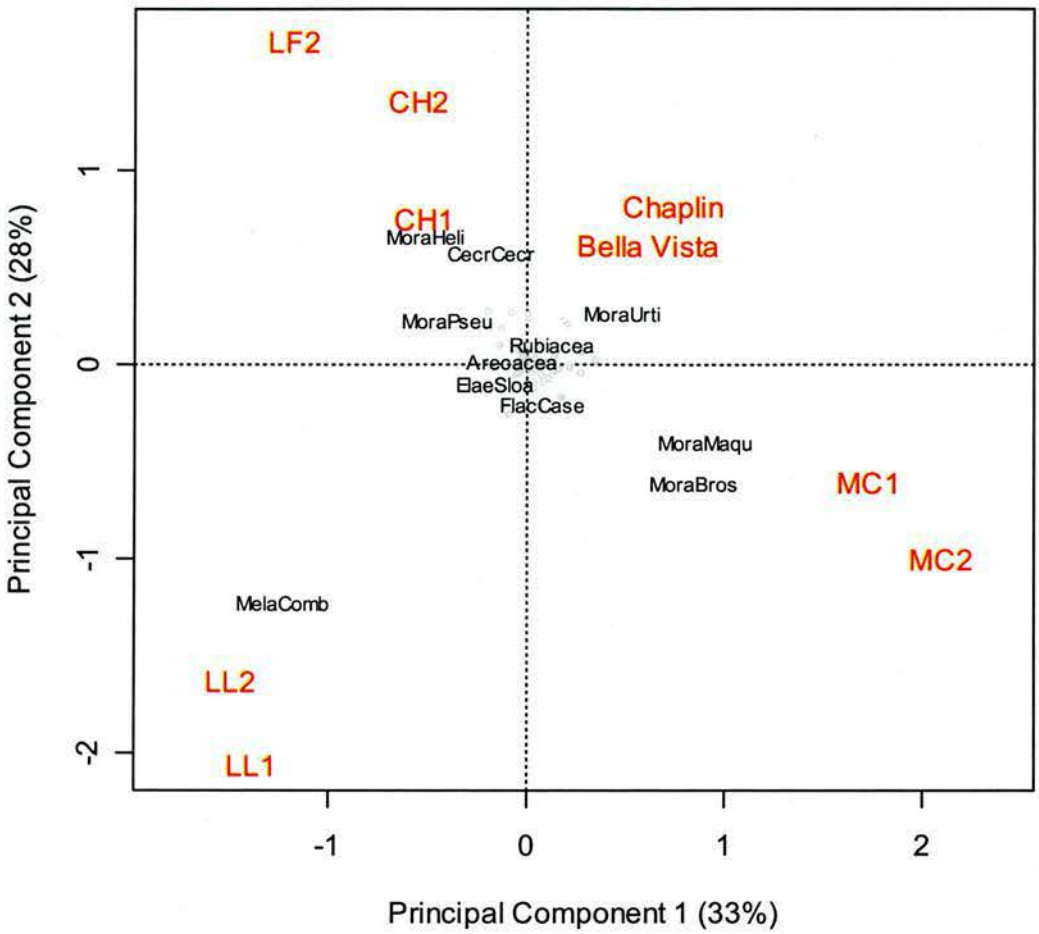

Fig. 3.5-6: a) Quadrat ordination (PCA) of pollen trap and lake surface sample data within NKMNP showing the first two principal components. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraHeli	Moraceae *Helicostylis*
CecrCecr	Cecropiaceae *Cecropia*
MoraUrti	Moraceae/Urticaceae
MoraPseu	Moraceae *Pseudolmedia*
Rubiacea	Rubiaceae
Arecacea	Arecaceae
ElaeSloa	Elaeocarpaceae *Sloanea*
FlacCase	Flacourtaceae *Casearea*
MoraMaqu	Moraceae *Maquira*
MoraBros	Moraceae *Brosimum*
MelaComb	Melastomataceae/ Combretaceae

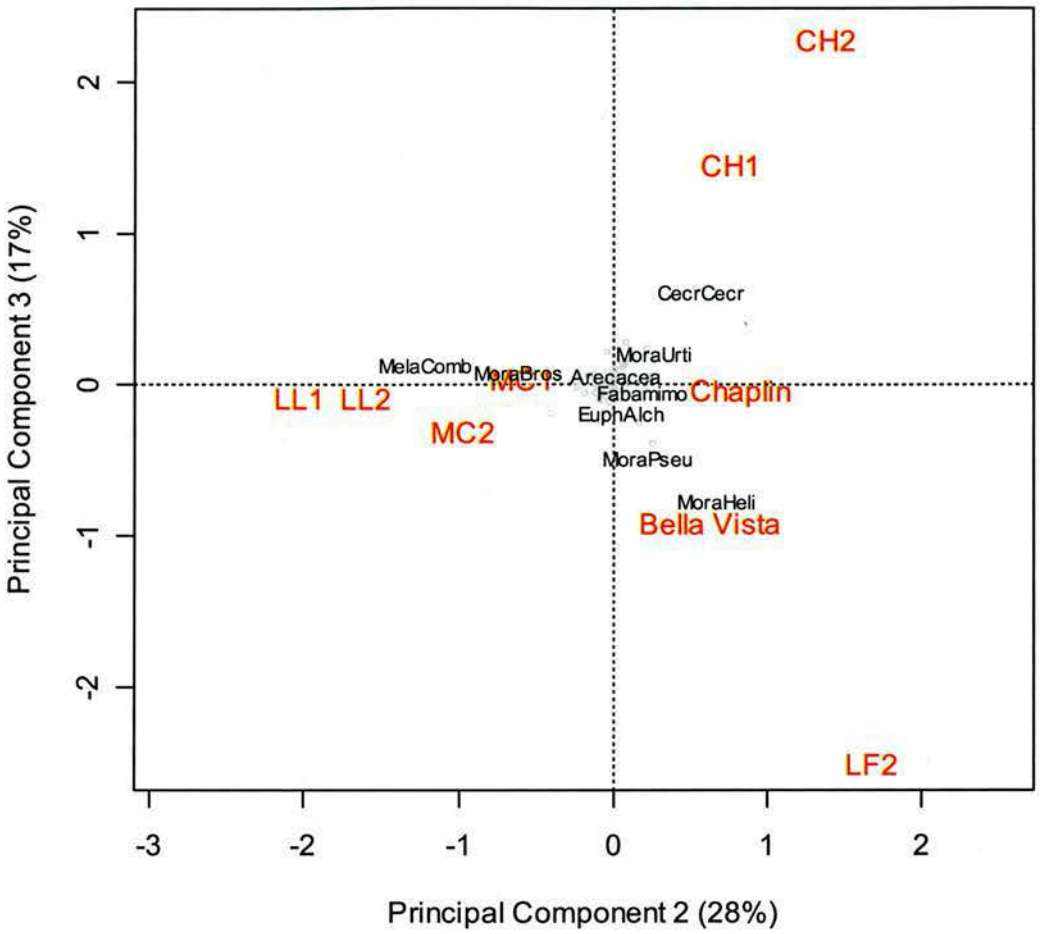

Fig. 3.5-6: b) Quadrat ordination (PCA) of pollen trap and lake surface sample data within NKMNP showing the second and third principal components. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraHeli	Moraceae *Helicostylis*
CecrCecr	Cecropiaceae *Cecropia*
MoraUrti	Moraceae/Urticaceae
MoraPseu	Moraceae *Pseudolmedia*
Fabamimo	fabaceae *Mimosa*
Arecacea	Arecaceae
EuphAlch	Euphorbiaceae *Alchornea*
MoraMaqu	Moraceae *Maquira*
MoraBros	Moraceae *Brosimum*
MelaComb	Melastomataceae/ Combretaceae

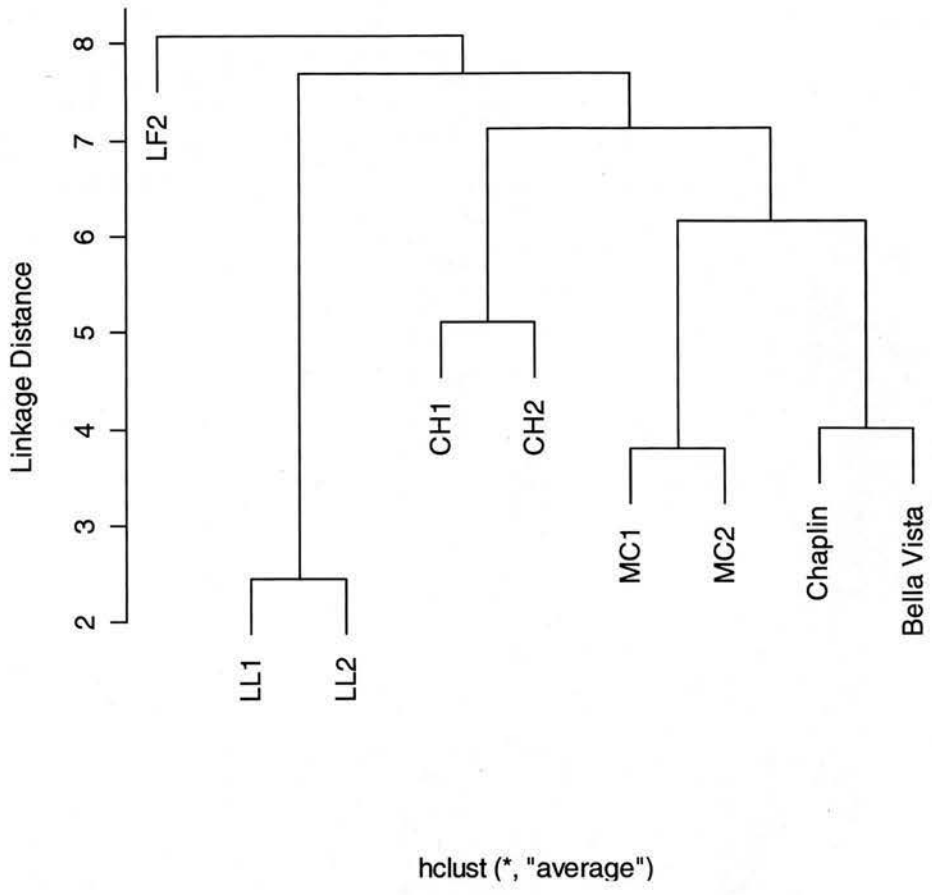

Fig. 3.5-6: c) Cluster analysis of pollen trap and lake surface sample data within NKMNP using the UPGMA classification technique. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

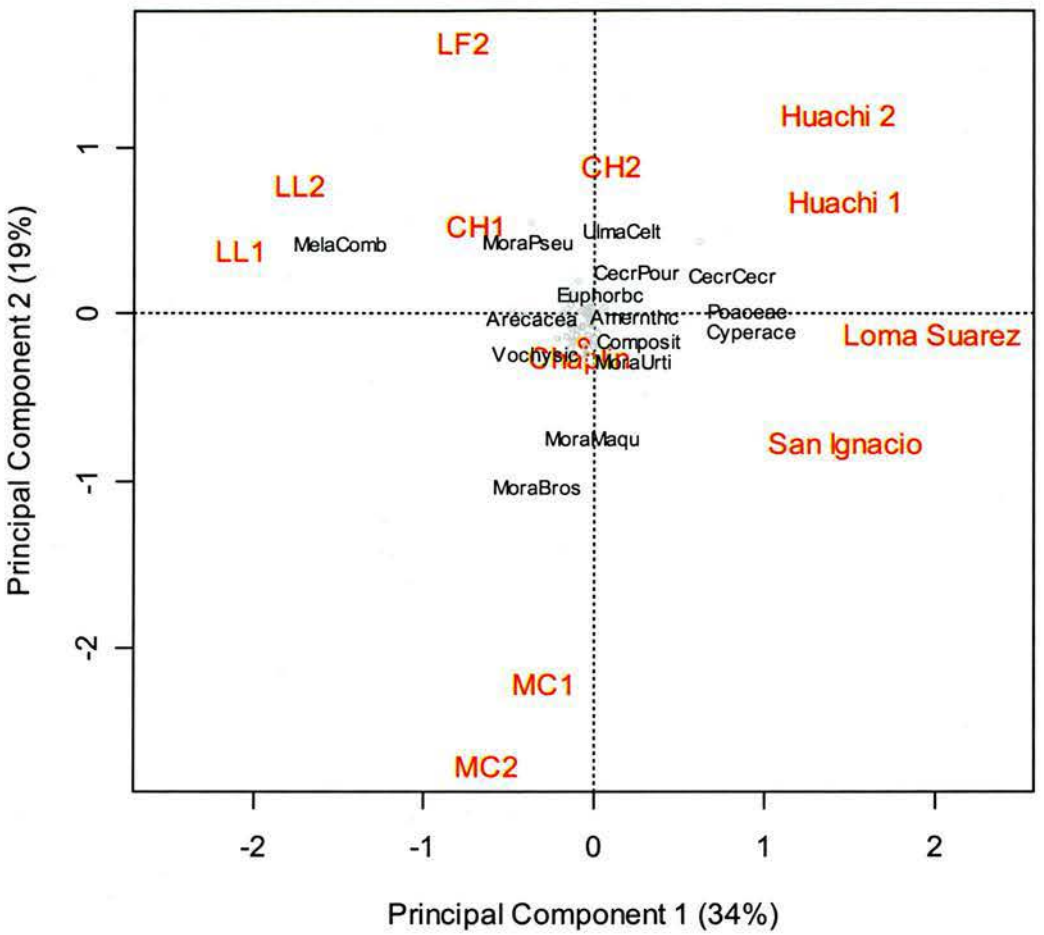

Fig. 3.5-6: d) Quadrat ordination (PCA) of all pollen trap and lake surface sample data within the study area. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraHeli	Moraceae *Helicostylis*	Composit	Compositae (Asteraceae)
CecrCecr	Cecropiaceae *Cecropia*	Vochysic	Vochysiaceae
MoraUrti	Moraceae/Urticaceae	Alternthc	Amaranthaceae *Allternanthera*
MoraPseu	Moraceae *Pseudolmedia*		
UlmaCelt	Ulmaceae *Celtis*		
Arecacea	Arecaceae		
ElaeSloa	Elaeocarpaceae *Sloanea*		
Cyperace	Cyperaceae		
MoraMaqu	Moraceae *Maquira*		
MoraBros	Moraceae *Brosimum*		
MelaComb	Melastomataceae/ Combretaceae		
CecrPour	Cecropiaceae *Pourouma*		
Poacea	Poaceae		

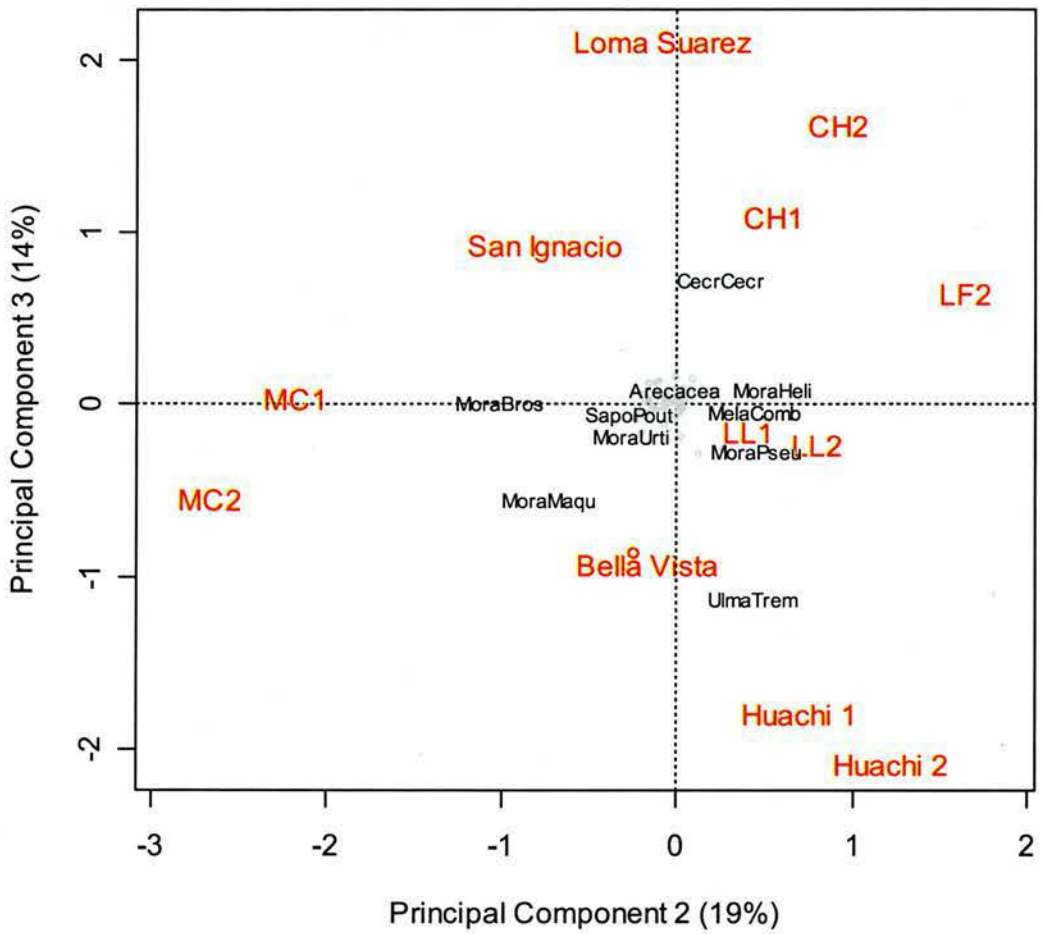

Fig. 3.5-6: e) Quadrat ordination (PCA) of all pollen trap and lake surface sample data within the study area. Grey dots represent genera that are included within the ordination analysis but are not listed for clarity. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

Key to represented taxa:

MoraHeli	Moraceae *Helicostylis*
CecrCecr	Cecropiaceae *Cecropia*
MoraUrti	Moraceae/Urticaceae
MoraPseu	Moraceae *Pseudolmedia*
SapoPout	Sapotaceae *Pouteria*
Arecacea	Arecaceae
UlmaTrem	Ulmaceae *Trema*
MoraMaqu	Moraceae *Maquira*
MoraBros	Moraceae *Brosimum*
MelaComb	Melastomataceae/ Combretaceae

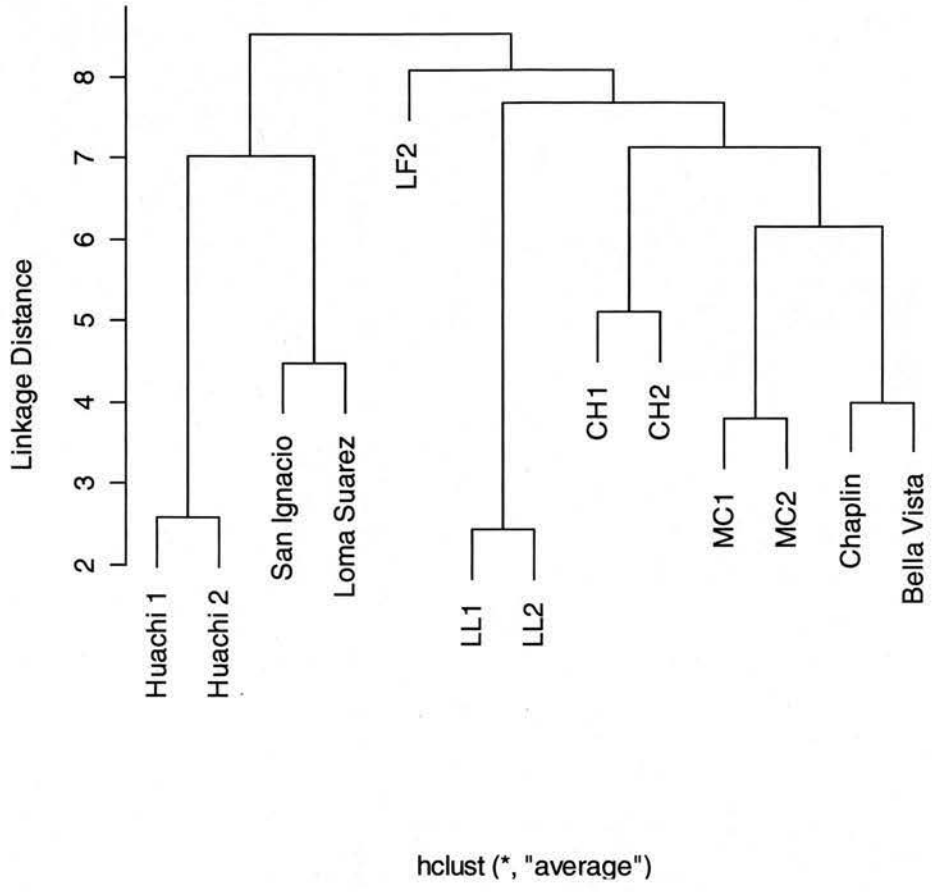

Fig. 3.5-6: f) Cluster analysis of all pollen trap and lake surface sample data within the study area using the UPGMA classification technique. MC 1 and 2 (Riparian forest plots at Monte Cristo), LL 1 and 2 (seasonally inundated raiforest plots at Las Londras), CH1 and 2 (*terra firme* liana rainforests plots at El Chore), LF 1 and 2 (*terra firme* moist evergreen rainforest plots at Los Fierros).

3.6 Discussion

3.6.1 *Floristic data*

Each of the four studied rainforests of NKMNP has a distinct floristic composition and can be readily differentiated using multivariate ordination analysis (Figs 3.5-4 (a, b, c)). The first principal component of a PCA on the floristic data represents levels of inundation where well-drained *terra firme* forests plot to the left of the ordination diagram and seasonally inundated and riparian forests to the right. This alignment of data along an inundation gradient is consistent with the distribution of rainforest communities in NKMNP. *Terra firme* liana forests are coincident with well-drained, dystrophic Oxisols that become dry towards the end of the dry-season (Killeen et al., 2002). In contrast, *terra firme* moist evergreen rainforests grow on well-drained Oxisols that remain moist throughout the dry season. Of the seasonally-flooded forests, riparian communities occupy elevated levees formed by sediment deposition on river banks and are consequently distinct from seasonally inundated floodplain forests that remain flooded throughout the wet season.

The Moraceae family is particularly diverse and abundant in NKMNP, including several species of *Pseudolmedia*, *Brosimum*, *Maquira*, *Sorocea* and *Ficus* and reaches its greatest diversity and abundance in flooded and riparian forest ecosystems (Killeen, 1998). Flood-tolerant canopy trees such as *Maquira coriacea* and *Brosimum lactescens* are well-represented in riparian forest communities, and trees adapted to more well-drained conditions, which include *Pseudolmedia* and *Helicostylis* are prominent in *terra firme* sites. *Brosimum lactescens* is a very important component of high-várzea (whitewater) forest communities across the

Amazon Basin (Wittman et al., 2006) and *Maquira coriacea* inhabits várzea (whitewater) and igapó (blackwater) flood plain forests throughout the Amazon, Orinoco and Río Paraguay Basins (Nebel et al., 2001b).

Of the families represented at NKMNP (Table 3.5-1; Fig. 3.5-4(b)), the most comon are are also found in rainforests elsewhere in the Amazon Basin. Moraceae, Arecaceae, Fabaceae (Leguminosae), Euphorbiaceae and Cecropiaceae dominate the rainforest inventories at NKMNP and are among the 16 most important families that characterise forests across the Amazon Basin (Wittman et al., 2006; Ter Steege et al., 2006). In general, rainforests at NKMNP are floristically most similar to those of western Amazonia, the ten most abundant genera of which are *Iriartea*, *Attalea*, *Otoba*, *Oenocarpus*, *Pseudolmedia*, *Ficus*, *Clarisia*, *Sapium*, *Spondias* and *Cecropia* (ter Steege et al., 2006). In contrast, none of the ten most abundant genera in the Guiana shield area of Amazonia are represented at NKMNP and our data are therefore consistent with the geographical gradient in tree composition stretching from the Guiana Shield in northeastern Amazonia to the Bolivian and Peruvian lowlands in southwestern Amazonia (Ter Steege et al., 2006; Wittman et al., 2006).

Species richness of the studied rainforest communities is also correlated with the underlying inundation gradient. Riparian and flood plain forests at Monte Cristo and Las Londras are significantly less species-rich per unit area than their *terra firme* counterparts at Los Fierros and El Chore. The former two communities contain 133 and 144 species ha^{-1}, respectively, while the latter correspondingly comprise 182 and 229 species ha^{-1}. Such differences in species richness are consistent with those exhibited by rainforest communities across the Amazon Basin (Nebel et al., 2001a; Worbes, 1997; Balslev et al., 1987) and may be explained by two principal

physiological stresses, which are imposed upon floodplain and riparian rainforests by the seasonal flooding regime of lowland rivers. First, erosion and deposition of alluvial sediments of dynamic lowland rivers reduces seedling recruitment and consequently species richness. Second, maintenance of anaerobic conditions over long periods of inundation causes root-anoxia and a reduction in a plant's metabolic rate (Wittman et al., 2006). Species richness observed within the park's upland *terra-firme* rainforests is also comparable with central Amazonian upland forests (much of which is dominated by the Madeira-Tapajós moist forest ecoregion), which comprise on average 179 to 285 species ha^{-1} (de Oliveira and Nelson, 2001; Ter Steege et al., 2003) and is greater than that exhibited by forests in eastern Amazonia, which consist of 117 to 120 species ha^{-1}. However, rainforests within NKMNP are not as species rich as those in western Amazonia, which hold up to 300 species ha^{-1} (Gentry, 1987; ter Steege et al., 2003).

In summary, modern forest communities within NKMNP can be readily distinguished from each other by their floristic composition at both species and genus levels. When compared with rainforest communities across the Amazon Basin, the forests at NKMNP are most similar to those occupying the southwestern end of a geographic gradient stretching from the Guiana Shield to southeastern Amazonia. The Moraceae family is particularly diverse in NKMNP and flooded and well-drained rainforests differ significantly from one another in terms of their species richness. The ability to floristically differentiate communities at the genus level is particularly important for the harmonization and comparison of datasets with palynological data, because pollen grains themselves can generally only be identified to the family and genus levels. Not only does such taxonomic harmonization permit

numerical comparisons between Neotropical pollen records and their parent communities in NKMNP, but since floristic data are consistent with studies across much of the Amazon Basin, we would expect similar comparisons to be possible elsewhere. Moreover, operating at the genus level has the additional benefit that up to 95% of individuals are correctly identified to genus level providing confidence in the results obtained (Ter Steege et al., 2006).

3.6.2 *Pollen data*

All four studied rainforest communities are readily differentiated by their pollen rain using multivariate ordination analysis, demonstrating that beta-diversity exhibited by the floristic data is well-captured by the pollen spectra (Figs. 3.5-4 (d, e, f)). Moreover, pollen spectra are spatially and temporally consistent within a given forest type, lending confidence in their use as modern analogue signatures to which the fossil pollen record may be numerically compared. Of the more abundant taxa, *Celtis*, *Helicostylis*, *Pseudolmedia*, *Brosimum*, *Maquira* and Melastomataceae/Combretaceae dominate both percentage (Fig. 3.5-2) and concentration (Fig. 3.5-3) pollen diagrams and are key to the differentiation of the four rainforests. *Celtis* is particularly prominent in *terra firme* liana forests, *Helicostylis* and *Pseudolmedia* in *terra firme* moist evergreen forests, Melastomataceae/Combretaceae in seasonally inundated forests and *Brosimum* and *Maquira* in riparian forest communities. *Helicostylis*, *Pseudolmedia*, *Brosimum* and *Maquira* are constituent genera of the predominantly wind-pollinated Moraceae family and their prominence in the pollen rain mirrors their abundance in floristic inventories. Indeed, considering the dominance of this family in southwest

Amazonian pollen records (Burbridge et al., 2004; Bush et al., 2007; Gosling et al., 2005), it is imperative that palynological studies focus on the pollen-taxonomy of this family across the Amazon Basin in order to extract more detailed ecological information from fossil pollen records (See Burn and Mayle, in press). Of the less abundant taxa, *Pouteria* and *Symmeria* are notable components of riparian forest pollen spectra, *Cordia* and *Byrsonima* of liana forest, *Inga* and *Sloanea* of floodplain forest and *Tapirira* and *Hyeronima* of moist evergreen forest pollen spectra.

3.6.2.1 Effect of pollination biology on pollen spectra

The effect of pollination syndrome on the resulting pollen spectrum is readily visualised when the ordination diagrams of both floristic and pollen datasets are compared (Figs. 3.5-4 (a – f)). Inspection of these diagrams reveals that the differentiation of rainforests is driven by different taxa in each dataset. Within seasonally flooded forests at Las Londras, for example, *Rinoreocarpus* (Violaceae) dominates the floristic dataset and drives the separation of this ecosystem in the ordination diagram (Fig. 3.5-4 (b)). The differentiation of the pollen spectra from the same forest is driven by the abundance of Melastomataceae/Combretaceae pollen (Fig. 3.5-4 (e)). Genera of the Violaceae family are cleistogamous. Their pollen is generally not released into the atmosphere and consequently does not become part of the forest's pollen rain. In contrast, the Melastomataceae family is bee-pollinated and is particularly well-dispersed since buzz-pollination releases large amounts of pollen into the surrounding environment (Bush and Riviera, 2001). Of this family, *Miconia* is well-represented within the floristic inventories of seasonally-inundated forest communities (Table 3.5-1) and consequently dominates the pollen spectrum driving the separation of this site from other rainforest communities within the ordination

diagram. Although Melastomataceae and Combretaceae pollen grains cannot yet be morphologically differentiated within NKMNP, we are confident that this category represents *Miconia* as it is extremely abundant within the floristic inventories at Las Londras and, since it is not wind-pollinated, it is unlikely to have come from further afield.

The dominance of wind-pollinated taxa in Amazonian lowland pollen assemblages results in further loss of floristic information since these taxa disperse large amounts of pollen that flood the resulting pollen signature. Furthermore, many cleistogamous and hermaphroditic taxa are not represented at all because their pollen is not released into the environment. Differentiation of riparian and *terra firme* plots is driven mainly by the abundance of wind-pollinated taxa (Fig. 3.5-2; Fig. 3.5-3; Fig. 3.5-4(e)), which represent just 7% of rainforest species within the park. In Neotropical rainforests elsewhere, anemophilous taxa have been shown to represent just 2-3% of rainforest species (Bush et al., 2001; Bawa and Opler, 1975). At NKMNP, the constrained ordination of vegetation and pollen datasets demonstrates that anemophilous taxa, which include genera of the Moraceae, Ulmaceae, Cecropiaceae and Anacardiaceae families, significantly control the separation of the pollen trap data (Figs 3.5-5 (e, f)). The pollen spectra obtained from riparian forests are dominated by the abundance of *Maquira* and *Brosimum* distinguishing them from the *terra firme* tall moist evergreen forest plots at Los Fierros, which are dominated by *Helicostylis*, *Pseudolmedia* and *Tapirira* pollen. *Celtis*, *Pourouma* and *Cecropia* are wind-pollinated pioneer species and are well represented in liana forest plots. By their very nature dioecious wind-pollinated species produce large quantities of pollen that are dispersed widely in order to increase the probability of sexual reproduction.

It is clear that these taxa dominate the pollen spectra of rainforests at NKMNP and our results support the contention put forward by Bush et al. (2001) that wind-pollination is favoured within the pollen record.

Plants whose pollination biology is hermaphroditic or cleistogamous may be well-represented in the floristic inventories but under-represented in the pollen rain because their pollen is less well dispersed. If such pollen is found within the pollen rain, its presence may provide significant ecological information with regards to the local vegetation and aid palynological characterisation. The genus *Pouteria* for example, is an hermaphroditic genus of the Sapotaceae family. It is extremely well-represented in seasonally inundated and riparian forest communities in NKMNP (Table 3.5-1), yet its representation in pollen spectra of riparian forests at Monte Cristo and floodplain forests at Las Londras (Fig. 3.5-2) is comparatively low accounting for around 1-2% of the pollen rain. Nevertheless, its pollen is restricted to these sites and consequently aids the differentiation of flooded forest communities from well-drained *terra firme* forests. Similarly, *Cordia* has a hermaphroditic pollination strategy and is only represented as *Cordia alliodora* in liana forests of the park. While *Cordia* grows under a wide variety of ecological conditions, the species does not tolerate water logging (Boshier et al., 1995). Its occurrence in pollen assemblages in surface sediments at Laguna Bella Vista and Laguna Chaplin is therefore strongly indicative of the local presence of liana forests. *Symmeria paniculata* is another indicator species that does not disperse pollen widely. It is restricted to blackwater-flooded rainforests and is highly flood-tolerant (Ferreira and Stohlgren, 1999). Within the park it is abundant within riparian forests at Monte

Cristo, where it accounts for less than 1% of the pollen rain of this plot, as well as in surface sediments at Laguna Bella Vista.

3.6.2.2 Pollen Accumulation Rates (PAR)

Investigation of mean pollen deposition to each of the studied rainforest communities suggests *terra firme* communities are more prolific in terms of their pollen productivity than flooded forests (Fig. 3.5-1). There may therefore be considerable potential for differences in the pollen concentration of different rainforest communities' data to be used to corroborate pollen percentage data. Average pollen accumulation rates exhibited by *terra firme* evergreen communities at Los Fierros NKMNP (10476 grains cm^{-2} $year^{-1}$; 95% CI: 8389 – 13391 grains cm^{-2} $year^{-1}$) are significantly higher than those obtained from liana (7433 grains cm^{-2} $year^{-1}$; 95% CI: 5909 – 9374 grains cm^{-2} $year^{-1}$), inundated (5806 grains cm^{-2} $year^{-1}$; 95% CI: 4859 – 6941 grains cm^{-2} $year^{-1}$) and riparian forests (4401 grains cm^{-2} $year^{-1}$; 95% CI: 3754 – 5159). Apart from a small degree of overlap of the confidence intervals, it is clear that there is a significant difference between pollen deposition rates in *terra firme* evergreen rainforest and riparian forest communities, which may be of great value for the interpretation of Amazonian fossil pollen records.

The gradient of pollen deposition exhibited by rainforest communities of NKMNP is therefore broadly correlated with level of inundation and species richness. High species richness recorded within the well-drained forests at Los Fierros and El Chore (182 and 229 species respectively) is coincident with high pollen deposition rates whereas low species richness exhibited by seasonally flooded and riparian forests at Las Londras and Monte Cristo (144 and 133 species) is related to low pollen productivity. We suggest the low pollen productivity exhibited by

flooded forest communities is a result of species being subjected to physiological stresses that are induced by long periods of inundation during the wet season. Prolonged inundation causes root-level anoxia and reduces a plant's metabolic rate, in turn constraining pollen productivity (Wittman et al., 2006). This contention is supported by empirical studies on floodplain forests in central Amazonia, which demonstrate that ecological processes such as productivity, plant distribution and reproductive biology are constrained by the duration and annual regularity of flooding (Megonigal et al., 1997; Ferreira and Prance1998; Ferreira and Stohlgren, 1999). While the degree of inundation is the result of both climatic and geomorphic/hydrologic controls, there is not sufficient evidence, within 95% confidence intervals, to suggest that annual climate variability is significantly manifested in the pollen deposition data, in contrast to the findings of Gosling et al. (2005) from *terra firme* rainforest, dry forest, and savanna plots, or studies from temperate settings (e.g. Bennett and Hicks, 2005; Sjogren et al., 2006).

Pollen deposition values are low at each of the sites when compared with those obtained elsewhere across Amazonia. Bush and Riviera (1998) recorded 22,429 grains cm^{-2} $year^{-1}$ from evergreen rainforests at Barro Colorado Island (BCI), Panama. However, the distribution of mean values was skewed at BCI (median = 7824 grains cm^{-2} $year^{-1}$) and no confidence limits were provided. Pollen deposition in moist evergreen rainforests at Los Fierros is consistent with accumulation rates obtained from undisturbed Atlantic rainforests along the Brazilian coast (12456 grains cm^{-2} $year^{-1}$; Behling and Negrelle, 2006).

The application of pollen deposition values to the interpretation of the fossil pollen record may be of great value when combined with analogue matching

techniques. However, the comparison of pollen trap and lake sediment data is not straightforward because each contains pollen deposited over different time scales. Indeed, estimates of annual pollen concentration from Amazonian lowland lake records are marred by the relatively poor temporal resolution that can be obtained (E.g. Colinvaux et al., 1996; Mayle et al., 2000; Bush et al., 2004; Bush et al., 2007). A second problem is that taphonomic processes differ considerably between deposition into pollen trap samples and into a lake, which may not necessarily affect the taxonomic composition of the resulting pollen assemblages, but could affect deposition rates, especially within the complex hydrological network of NKMNP. Moreover, there are considerable differences in the extent of the pollen source area between both depositional environments, which would affect pollen flux estimates. Nevertheless, the differences in pollen deposition exhibited by *terra firme* and flooded rainforest communities is considerable and the extent to which this kind of information can be extracted from fossil pollen records needs to be tested. Indeed, progress in the application of pollen trap deposition rates to the fossil pollen record in northern Sweden has been made. Comparisons of long-term average pollen influx measured from limnic sediments have been shown to be consistent with pollen trap deposition data despite differences in the depositional environments (Hicks, 2001).

3.6.3 *Comparison of pollen trap and lake surface samples*

The numerical comparison of pollen rain data with lake surface samples at Laguna Bella Vista and Laguna Chaplin suggests that, in terms of taxonomic composition, the pollen trap spectra of riparian forests closely match those obtained from the sediment-water interface at both lakes. However, inspection of the first principal

component within the ordination diagram suggests significant elements of *terra firme* rainforest including *Helicostylis*, *Pseudolmedia* and *Pourouma*, are also present in the surface samples. The samples at Laguna Bella Vista and Laguna Chaplin therefore represent a composite signal comprising elements of riparian and *terra firme* rainforest. This conclusion is supported by the presence of *Symmeria* and *Cordia* within the surface assemblages, each representing riparian and liana forests, respectively. Furthermore, these pollen trap-lake surface sample comparisons demonstrate that the surface pollen assemblages at these lakes accurately reflects the mosaic of rainforest ecosystems surrounding the lakes today; i.e. seasonally-flooded forests in the floodplain of Río Paraguá and *terra firme* liana forests (Laguna Bella Vista) and moist evergreen tall rainforest (Laguna Chaplin; Fig. 3.3-1) in higher non-flooded areas.

Numerical analysis of all trap and surface sediment samples reveals a clear separation of pollen spectra obtained from NKMNP that plot to the left of the ordination diagram and surface sediment samples from the Llanos de Moxos ecosregion (Beni Basin) that plot to the right (Fig. 3.5-6 (d)). The principal drivers of this separation may be attributed to the abundance of *Cecropia*, Poaceae and Cyperaceae at Laguna Loma Suarez and Laguna San Ignacio and that of *Trema* at Laguna Huachi. The pioneer genus *Cecropia* is well-adapted to disturbed open environments throughout the Neotropics but is particularly adapted to early-successional vegetation communities developing on alluvial sediments deposited by the Río Mamoré and represents a significant proportion of that vegetation (Maldonando and Beck, 2004). The provenance of grass and sedge pollen within lakes of the Llanos de Moxos ecoregion is unclear, and likely comprises both aquatic

vegetation, growing in the littoral zones of the lakes, and seasonally-inundated savannah communities beyond the gallery forests lining the Río Marmoré. Laguna Loma Suarez was the smallest lake sampled and the proportion of aquatic to non-aquatic pollen was expected to be greater at this site. A visual survey of the littoral zone surrounding the lake further indicates a dense littoral zone comprising numerous aquatic grasses and sedges. It is likely, therefore that much of the grass signal comprises aquatic grasses. In contrast, Laguna San Ignacio is a larger lake and aquatic grasses are less likely to be represented at this site because the regional pollen rain will comprise a greater proportion of the pollen sum (Jacobson and Bradshaw, 1981). Laguna Huachi, like Lagunas Bella Vista and Chaplin, is situated within *terra firme* rainforest of the Madeira-Tapajós moist forest ecoregion between NKMNP and the Llanos de Moxos ecoregion (Beni Savannas). Investigation of the second principal component reveals that, apart from the dominance of *Trema* within the pollen assemblages, it shares a similar pollen signature with *terra firme* liana forest sites at NKMNP (Fig. 3.5-6(e)) and is consistent with the geographic distribution of these forests within the ecoregion (Killeen, 1998).

There is a lot of debate regarding the extent to which pollen trap data is applicable to the interpretation of the fossil pollen record (Bush and Riviera, 1998; Bennett and Hicks, 2001; Hicks, 2001) due to differences in the depositional environment and the operation of different taphonomic processes. The pollen evidence presented here suggests that differences in the depositional environment have little impact on the resulting pollen assemblages. If the depositional environment was an important control on the composition of the resulting pollen assemblages then lake surface samples within and outside the park would be

expected to cluster together within an ordination analysis since they are lake sites and their taphonomic pathways are similar. However, the clustering together of both trap and lake pollen assemblages of NKMNP and their subsequent separation from lake surface spectra of the Beni basin (Fig. 3.5-6 (f)) suggests that the taxonomic composition of samples overrides the influence of depositional environment. This result provides substantial support for direct numerical comparison of pollen trap spectra obtained from undisturbed rainforest communities with lake sediment pollen assemblages. Such direct comparison of trap data with the sedimentary record also provides support for the application of an analogue matching approach to palaeoecology in lowland rainforest regions.

3.6.4 *Implications for Amazonian palaeoecology*

The differentiation of Amazonian rainforest communities within NKMNP has important implications for Amazonian palaeoecology outwith the park. For example, rainforest pollen assemblages obtained from lake sediments in eastern Amazonia are remarkable similar to riparian forest pollen spectra of NKMNP. For example, pollen assemblages obtained from Holocene lake sediments at Lago Tapajós situated within the Madeira-Tapajós moist forest ecoregion in eastern Amazonia (Irion et al., 2006), share very similar characteristics to riparian forests at NKMNP. The authors interpreted early Holocene pollen assemblages, deposited during the initial formation of the lake, as representing closed-canopy lowland forest characteristic of both riparian forest and *terra firme* elements. The *terra firme* elements, however, comprised the following taxa: *Alchornea*, *Brosimum*, *Pouteria*, *Sapium*, *Sebastiana*, *Socratea*, *Symmeria* and *Waltheria*. When compared with pollen signatures obtained

from lowland forests at NKMNP, it is clear that this combination of taxa actually characterises riparian forest communities. On this basis alone, Irion et al. (2006) present no palynological evidence to support the presence of *terra firme* rainforest during the Holocene at this site. While absence of pollen spectra characteristic of *terra firme* rainforests does not necessarily mean absence of *terra firme* rainforest *per se*, it is clear that the sediments of Rio Tapajós only record pollen spectra of forest communities lining the Tapajós River and the site cannot therefore be invoked to support the presence of spatially extensive closed canopy rainforest communities during the early Holocene period.

The potential applicability of our results for the interpretation of Quaternary vegetation records elsewhere in Amazonia is therefore clear. Indeed, if pollen assemblages of eastern Amazonia are similar to those within NKMNP then these results may also be of particular importance for the interpretation of glacial fossil pollen assemblages recorded in sediments of the Amazon Fan (Haberle 1997; Haberle and Maslin, 1999), which may help resolve much of the controversy surrounding the Quaternary vegetation dynamics of Amazonia's rainforests. The persistent abundance of Moraceae/Urticaceae pollen in the sedimentary record of the Amazon Fan throughout the last glacial and Holocene period is suggested by some to indicate that the Amazon Basin was covered by extensive rainforest throughout this period (e.g. Haberle and Maslin; Colinvaux et al., 2000; Bush et al., 2004). Others have suggested its presence may simply reflect gallery or riparian forests lining the rivers during glacial periods, which masked pollen from savannahs or dry forests beyond, consistent with the glacial aridity hypothesis (Haffer, 1969; Haffer and Prance, 2001; Prado and Gibbs, 1993; Pennington et al., 2000; Van der Hammen and

Absy, 1994). Improvements in the pollen taxonomy of the Moraceae family (Burn and Mayle, in press) and the characterisation of rainforest communities in NKMNP demonstrates that riparian and *terra firme* rainforests can be differentiated from each other palynologically and may therefore help determine the exact nature of the rainforest pollen signal within the Amazon Fan record. If, for instance, the Moraceae/Urticaceae curve comprised *Helicostylis* pollen and was further associated with taxa indicative of well-drained conditions such as *Celtis* and *Cordia*, this would provide strong support for the presence of spatially extensive *terra firme* rainforests and the continuous forest hypothesis (Colinvaux et al., 2000) since these taxa are ecologically restricted to *terra firme* plant communities in NKMNP. If, however, the Moraceae/Urticaceae pollen signal was found to comprise riparian indicator taxa such as *Maquira* or *Brosimum*, as well as indicator taxa from other families such as *Symmeria* and *Sapium* then this would suggest the Amazon Fan sediments record a predominantly riparian signal, which would be consistent with both the continuous forest hypothesis (Colinvaux et al., 2000) and the glacial aridity hypothesis (Haffer, 1969; Prado and Gibbs, 1993; Haffer and Prance, 2001; Pennington et al. 2000).

3.7 Conclusions

Multivariate and cluster analysis performed on floral biometric and pollen rain datasets obtained from four distinct Amazonian rainforest communities of NKMNP demonstrates that *terra firme* evergreen, *terra firme* liana, seasonally inundated and riparian rainforests can be differentiated from each other, floristically and palynologically. Pollen spectra may be characterised by both abundant and less abundant taxa. Of the abundant taxa, *Celtis* is particularly prominent in *terra firme*

liana forests, *Helicostylis* and *Pseudolmedia* in *terra firme* moist evergreen forests, Melastomataceae/Combretaceae in seasonally inundated forests and *Brosimum* and *Maquira* in riparian forest communities. Less abundant indicator taxa include *Pouteria* and *Symmeria*, which are notable components of riparian forest pollen spectra, *Cordia* and *Byrsonima* of liana forest, *Inga* and *Sloanea* of floodplain forest and *Tapirira* and *Hyeronima* of moist evergreen forest communities. The strong beta-diversity exhibited by the floristic data is also captured, and recognised, within the pollen rain and is controlled by underlying edaphic/hydrologic conditions that determine species richness, floristic composition and pollen productivity. The presence of pollen within trap assemblages is determined by the pollination syndrome of constituent species. Wind-pollinated taxa including genera of the Moraceae, Ulmaceae and Cecropiaceae families dominate pollen spectra and represent just 7% of rainforest genera. Habitat-specific genera of the Moraceae family include *Brosimum*, *Maquira*, *Pseudolmedia* and *Helicostylis*, each of which are particularly well-represented in both floristic and pollen datasets are crucial for the palynological differentiation of rainforests. Non-dioecious pollen taxa provide important ecological information about the local surroundings but are poorly represented within pollen spectra. Mean pollen influx to each of the rainforest communities is positively correlated with species richness and negatively correlated with degree of inundation.

Riparian forest communities represent the closest modern analogue for pollen assemblages obtained from surface sediment samples from lakes within NKMNP; however, elements of *terra firme* forests also constitute a significant proportion of these assemblages. The prominence of flooded and *terra firme* pollen spectra within

these surface samples is congruent with the present day geographic distribution of rainforest ecosystems within the park lending confidence for the applicability of modern pollen trap spectra to the fossil pollen record. There is a clear separation of pollen trap and surface sediment spectra obtained from NKMNP from those obtained from lakes within gallery forests of the Beni savanna ecoregion reflecting floristic differences between gallery forests of the Beni Basin and rainforests of NKMNP. *Trema* pollen dominates the pollen spectra at Laguna Huachi; however, a *terra firme* forest pollen signal, similar to that obtained from NKMNP, is strongly represented suggesting that the *terra firme* rainforest signature is consistent throughout the Madeira-Tapajós moist forest ecoregion. We have also demonstrated that pollen trap data may be directly compared with lake surface samples within ordination analyses and that differences in the depositional environment has little impact on the composition of the resulting pollen signatures.

Improvements in the pollen taxonomy of key genera of the Moraceae family (Burn and Mayle, in press) as well as the palynological characterisation of different rainforest communities within NKMNP may be applied to extract greater ecological information from fossil pollen records across the Amazon Basin. The extent to which rainforest pollen spectra of NKMNP may be compared with fossil pollen assemblages across the Amazon Basin has been illustrated by their comparison with pollen assemblages of early Holocene sediments of Lago Tapajós in eastern Amazonia. We suggest that pollen taxa documented as '*terra firme*' elements (*Alchornea*, *Brosimum*, *Pouteria*, *Sapium*, *Symmeria*) by the authors actually represent riparian forest taxa and that there is no palynological evidence to support the presence of the spatially more extensive *terra firme* rainforest during the

Holocene at this site. Since we are able to differentiate *terra firme* from seasonally flooded and riparian forests and we have shown that our data are applicable to fossil pollen sites in eastern Amazonia, our data could therefore also be of importance for the interpretation of glacial fossil pollen assemblages of the Amazon Fan, to determine whether the inferred rainforest pollen taxa represent *terra firme* or flooded forest communities, a subject that remains considerably controversial (Colinvaux et al., 2000; Anhuf et al., 2006). Indeed, if a riparian forest pollen signature is detected within glacial sediments of the Amazon Fan, this would be consistent with the glacial aridity hypothesis of Haffer (1969) and Haffer and Prance (2001) and the continuous forest hypothesis (Colinvaux et al., 2000), since neither the presence of savanna nor extensive rainforest cover could therefore be demonstrated during this period. In contrast, if pollen spectra of *terra firme* rainforest communities were detected within the sediments, this would provide further support for the continuous forest hypothesis (Colinvaux et al., 1996; Bush et al., 2004; Bush et al., 2007).

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3.9 References

Anhuf, D., Ledru, M. P., Behling, H., Da Cruz, F. W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J. A., De Oliveira, P. E., Pessenda, L.,

Siffedine, A., Albuquerque, A. L. and Dias, P. L. D. (2006). Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeography Palaeoclimatology Palaeoecology* **239**(3-4): 510-527.

Balslev, H., Lutteyn, J., Yllgaard, B., Holm-Nielsen, L. (1987). Composition and structure of adjacent unflooded and floodplain forest in Amazonian forests *Botanical Gazette* **111**: 413-425.

Bawa, K. S. and Opler, P. A. (1975). Dioecism in tropical forest trees. *Evolution* **31**: 52-63.

Beerling, D. J. and Mayle, F. E. (2006). Contrasting effects of climate and CO_2 on Amazonian ecosystems since the last glacial maximum. *Global Change Biology* **12**(10): 1977-1984.

Behling, H. (2002). Carbon storage increases by major forest ecosystems in tropical South America since the Last Glacial Maximum and the early Holocene. *Global and Planetary Change* **33**: 107-116.

Behling, H. and Negrelle, R. R. B. (2006). Vegetation and pollen rain relationship from the tropical Atlantic rain forest in southern Brazil. *Brazilian Archives of Biology and Technology* **49**(4): 631-642.

Bennett, K. D. and Hicks, S. (2005). Numerical analysis of surface and fossil pollen spectra from northern Fennoscandia. *Journal of Biogeography* **32**(3): 407-423.

Birks, H. J. B. (1986). Numerical Zonation, comparison and correlation in Quaternary pollen-stratigraphical data. In BE Berglund (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*: 743-774. John Wiley: Chichester.

Birks, H. J. B. and Gordon, A. D. (1985). Numerical Methods in Quaternary Pollen Analysis. Academic Press: London.

Boshier, D. H., Chase, M. R. and Bawa, K. S. (1995). Population-Genetics of Cordia-Alliodora (Boraginaceae), a Neotropical Tree .2. Mating System. *American Journal of Botany* **82**(4): 476-483.

Burbridge, R. E., Mayle, F. E. and Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* **61**(2): 215-230.

Burn, M. B. and Mayle, F. E. (in press). Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Review of Palaobotany and Palynology*.

Bush, M. B. (2002). On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177**(1-2): 5-17.

Bush, M. B., De Oliveira, P. E, Colinvaux, P. A., Miller, M. C. and Moreno, J. E. (2004). Amazonian paleoecological histories: One hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214**(4): 359.

Bush, M. B. and Rivera, R. (1998). Pollen Dispersal and Representation in a Neotropical Rain Forest. Global Ecology and Biogeography Letters 7, 379-392.

Bush, M. B. and Rivera, R. (2001). Reproductive ecology and pollen representation among neotropical trees. *Global Ecology and Biogeography* **10**(4): 359-367.

Bush, M. B., Silman, M. R. and Listopad, C. M. (2007). A regional study of Holocene climate change and human occupation in Peruvian Amazonia. *Journal Of Biogeography* Special Issue (Amazonian climate change and settlement): 1-15.

Bush, M. B. and Weng, C. Y. (2007). Introducing a new (freeware) tool for palynology. *Journal of Biogeography* **34**: 377-380.

Bush, M. B., Moreno, E., De Oliveira, P. E., Asanza, E. and Colinvaux, P. A. (2001). The influence of biogeographic and ecological heterogeneity on Amazonian pollen spectra. *Journal of Tropical Ecology* **17**: 729-743.

Colinvaux, P. A. and De Oliveira, P. E. (2000). Palaeoecology and climate of the Amazon basin during the last glacial cycle. *Journal of Quaternary Science* **15**(4): 347-356.

Colinvaux, P. A., De Oliveira, P. E. and Moreno, P. J. E. (1999). *Amazon Pollen Manual and Atlas*. Harwood Academic Publishers: Amsterdam.

Colinvaux, P. A., DeOliveira, P. E., Moreno, J. E., Miller, M. C., Bush, M. B. (1996). A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* **274**(5284): 85-88.

Cowling, S. A. (1999). Simulated effects of low atmospheric CO_2 on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecology and Biogeography* **8**: 81-93.

Cowling, S. A., Betts, R. A., Cox, P. M., Ettwein, V. J., Jones, C. D., Maslin, M. A. and Spall, S. A. (2005). Modelling the past and future fate of the Amazonian forest. In Y Malhi, OL Phillips (Eds.), *Tropical forests and global atmospheric change*. Oxford University Press: Oxford.

Cowling, S. A., Maslin, M. A. and Sykes, M. T. (2001). Paleovegetation Simulations of Lowland Amazonia and Implications for Neotropical Allopatry and Speciation. *Quaternary Research* **55**(2): 140.

de Oliveira, A. A. and Nelson, B. W. 2001. Floristic relationships of terra firme forests in the Brazilian Amazon. *Forest Ecology and Management* **146**(1-3): 169-179.

Duivenvoorden, J. F. (1996). Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica* **28**(2): 142-158.

Faegri, K. and Iversen, J. (1989). *Textbook of Pollen Analysis. fourth ed.* Wiley: Chichester.

Ferreira, L. V. (1998). Intraspecific variation in phenology in relation to flooding duration in *Eschweilera parvifolia* (Lecythidaceae) in central Amazonian floodplain forest. *Anais da Academia Brasileira de Ciências* **70**: 1-4.

Ferreira, L. V. and Prance, G. T. (1998). Structure and species richness of low-diversity floodplain forest on the Rio Tapajós, Eastern Amazonia, Brazil. Biodiversity and Conservation **7**: 585-596.

Ferreira, L. V. and Stohlgren, T. J. (1999). Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia* **120**(4): 582-587.

Gentry, A. H. (1987). Tree species richness in upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* **85**: 156-159.

Gosling, W. D., Mayle, F. E., Killeen, T. J., Siles, M., Sanchez, L. and Boreham, S. (2003). A simple and effective methodology for sampling modern pollen rain in tropical environments. *Holocene* **13**(4): 613-618.

Gosling, W. D. (2004). Characterization of Neotropical forest and Savannah Ecosystems by their Modern Pollen Spectra. Unpublished PhD Thesis.

Gosling, W. D., Mayle, F. E., Tate, N.J. and Killeen, T. J. (2005). Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research* **64**(3): 284-297.

Haberle, S., (1997). Upper Quaternary vegetation and climate history of the Amazon Basin: Correlating marine and terrestrial pollen records. In Flood, R.D., Piper, D.J.W., Klaus, A. and Peterson, L.C., (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 155: College Station, TX.

Haberle, S.G. and Maslin, M.A. (1999). Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon fan, ODP site 932. *Quaternary Research* **51**(1): 27-38.

Haffer, J. (1969). Speciation in Amazonian forest birds. Science **165**, 131-137.

Haffer, J., and Prance, G. T. (2001). Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. Amazoniana **16**, 579-607.

Hicks, S. (2001). The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. *Review of Palaeobotany and Palynology* **117**(1-3): 1-29.

Irion, G., Bush, M. B., de Mello, J. A. N., Stuben, D., Neumann, T., Muller, G., De Morais, J.O. and Junk, J. W. (2006). A multiproxy palaeoecological record of Holocene lake sediments from the Río Tapajós, eastern Amazonia. *Palaeogeography Palaeoclimatology Palaeoecology* **240**(3-4): 523-535.

International Plant Names Index, 2007. Published on the Internet http://www.ipni.org [accessed 9 January 2007].

Kent, M. and Coker, P. (1994). *Vegetation Description and Analysis: A Practical Approach*. John Wiley and Sons: Chichester.

Killeen, T. J. (1998). *Vegetation and flora of Noel Kempff Mercado National Park.* Conservation International, Washington, DC.

Killeen, T. J. and Schulenberg, T. S. (1998). *A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia.* : Conservation International, Washington, DC.

Killeen, T. J., Siles, T. M., Grimwood, T., Tieszen, L. L., Steininger, M. K., Tucker, C. J., and Panfil, S. (2003). Habitat heterogeneity on a forest-savanna ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): Implications for the long-term conservation of biodiversity in a changing climate. In Bradshaw, G.A. and Marquet, P.A. (Eds.), How landscapes change: Human disturbance and ecosystem fragmentation in the Americas, Ecological Studies 162, Springer Verlag, Berlin.

Legendre, P. and Gallagher E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**(2): 271-280.

Leps, J. and Smilauer, P. (2003). *Multivariate Analysis of Ecological Data using CANOCO.* Cambridge University Press: Cambridge.

Maher, L.J. (1981). Statistics For Microfossil Concentration Measurements Employing Samples Spiked With Marker Grains. *Review Of Palaeobotany And Palynology* **32**(2-3): 153-191.

Maldonando, C. and Beck, S. G. (2004). Comunidades sucesionales a orillas del Río Mamoré. In M Pouilly, SG Beck, R Moraes, C Ibanez (Eds.), *Diversidad biologica en la llanura de inundacion del Río Mamoré*. Fundacion Simon I. Patino: Santa Cruz, Bolivia.

Mayle, F.E. and Beerling, D. J. (2004). Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography Palaeoclimatology Palaeoecology* **214**(1-2): 11-25.

Mayle, F. E., Beerling, D. J., Gosling, W. D. and Bush, M. B. (2004). Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society of London B* **359**: 499-514.

Mayle, F. E., Burbridge, R. and Killeen, T. J. (2000). Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**(5500): 2291-2294.

Mayle, F. E., Langstroth, R. P., Fisher, R. and Meir, P. (2007). Long-term forest-savanna dynamics in the Bolivian Amazon: Implications for conservation. *Philosophical Transactions of the Royal Society, B* **362**: 291-307.

Megonigal, J. P., Conner, W. H., Kroeger, S. and Sharitz, R. R. (1997). Aboveground production in Southeastern floodplain forests: A test of the subsidy-stress hypothesis. *Ecology* **78**(2): 370-384.

Morley, R. J. (2000). *Origin and Evolution of Tropical Rain Forests.* John Wiley and Sons: Chichester.

Nebel, G., Kvist, L. P., Vanclay, J. K., Christensen, H., Freitas, L. and Ruiz J. (2001a). Structure and floristic composition of flood plain forests in the Peruvian Amazon I. Overstorey. *Forest Ecology and Management* **150**(1-2): 27-57.

Nebel, G., Dragsted, J., Simonsen, T. R. and Vanclay, J. K. (2001b). The Amazon flood plain forest tree Maquira coriacea (Karsten) CC Berg: aspects of ecology and management. *Forest Ecology and Management* **150**(1-2): 103-113.

Oksanen, J., Kindt, R., Legendre, P. and O'Hara, R.B. (2007). Vegan: Community Ecology Package version 1.8-5. http://cran.r-project.org.

Olsen, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N, Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Louks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel ,W. W., Hedao, P. and Kassem, K. R. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* **51**: 933-938.

Pennington, R. T., Prado, D. E. and Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal Of Biogeography* **27**(2): 261-273.

Prado, D. E. and Gibbs, P. E. (1993). Patterns of species distribution in the seasonally dry forests of South America. Annals of the Missouri Botanical Gardens **80**, 902-927.

Prance, G. T. (1979). Notes on the Vegetation of Amazonia .3. Terminology of Amazonian Forest Types Subject to Inundation. *Brittonia* **31**(1): 26-38.

Prance, G. T. (1989). American Tropical Forests. In H Lieth, MJA Werger (Eds.), *Tropical Rain Forest Ecosystems. Ecosystems of the World 14B*: 99-132. Elsevier: Amsterdam.

Prentice, I. C. (1980). Multidimensional scaling as a research tool in Quaternary Palynology: a review of theory and methods. *Review of Palaeobotany and Palynology* **31**: 71-104.

Salvias Project (2007). Published on the Internet http://www.salvias.net [accessed 7 May 2007].

Roubic, D. W. and Moreno, P. J. E. (1991). Pollen and Spores of Barro Colorado Island. *Monographs in Systematic Botany* **36**(Missouri Botanical Garden).

Sioli, H. (1968). Hydrochemistry and geology in the Brazilian Amazon region. *Amazonica* **5**: 51-76.

Sjogren, P., van Leeuwen, J. F. N., van der Knaap, W. O. and van der Borg, K. (2006). The effect of climate variability on pollen productivity, AD 1975-2000, recorded in a Sphagnum peat hummock. *Holocene* **16**(2): 277-286.

Sneath, P. H. A. and Snokal, R. R. 1973. *Numerical Taxonomy*. Freeman: San Fransisco.

Stockmarr, J. (1971). Tablets with spores used in absolute pollen analysis. *Pollen Spores* **13**: 615-621.

R Development Core Team. (2007). R: A language and environment for statistical computing. R Foundation for statistical computing.

ter Braak, C. J. F. (1986). Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

ter Braak, C. J. F. and Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research* **18**: 93-138.

ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van der Hout, P., Daly, D. C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., De Oliveira, A. A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P. N., Mogollon, H. and Morawetz, W. (2003). A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation* **12**(11): 2255-2277.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J. F., Prevost, M. F., Spichiger, R., Castellanos, H., von Hildebrand, P. and Vasquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**(7110): 444-447.

Tian, H. Q., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich, J. V. K., Moore, B. and Vorosmarty, C. J. (1998). Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**(6712): 664-667.

Valdes, P. J. (2000). South American palaeoclimate model simulations: how reliable are the models? *Journal Of Quaternary Science* **15**(4): 357-368.

Van der Hammen, T. and Absy, M. L. (1994). Amazonia During the Last Glacial. *Palaeogeography Palaeoclimatology Palaeoecology* **109**(2-4): 247-261.

Weng, C. Y., Bush, M. B. and Silman, M. R. (2004). An analysis of modern pollen rain on an elevational gradient in southern Peru. *Journal Of Tropical Ecology* **20**: 113-124.

Willis, K. J. and McElwain, J. C. (2002). *The evolution of plants*. Oxford University Press. Oxford.

Wittmann, F., Schongart, J., Montero, J. C., Motzer, T., Junk, W. J., Piedade, M. T. F., Queiroz, H. L. and Worbes, M. (2006). Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* **33**(8): 1334-1347.

Worbes, M. (1997). The forest ecosystem of the floodplains. In WJ Junk (Ed.), *The central Amazon floodplain: ecology of a pulsating system*: 223-265. Springer: Berlin.

Chapter 4 Discussion and Conclusions

4.1 Introduction

The aims of this chapter are (a) to summarise the main results and conclusions outlined in chapters two and three and to develop the principal arguments further; (b) to outline the wider implications of the results for Amazonian palaeoecology; (c) to examine two fundamental assumptions that underpin the scientific basis of this thesis; and (d) to highlight potential opportunities for future research resulting from this study. To this end, the first section of this chapter will outline the principal aims, results and conclusions. The second section will examine wider implications of the palynological differentiation of rainforest communities for our understanding of Amazonian Quaternary vegetation dynamics. In particular, it will examine palaeoenvironmental implications for the Amazon Basin as a whole, discuss underlying assumptions and provide suggestions for future research in this field.

4.2 Principal aims and conclusions

The principal aim of this thesis is to characterise and differentiate the pollen spectra of four different rainforest communities in order to extract greater ecological detail from Amazonian fossil pollen records. To this end, the aims of this study were a) to differentiate between pollen of the constituent genera of the Moraceae and Urticaceae families which are represented within different kinds of rainforest community in NKMNP; (b) to characterise and differentiate four rainforest communities of NKMNP by their pollen rain; (c) to compare numerically these pollen signatures with floral biometric inventories to better understand pollen-vegetation relationships within rainforest settings and (d) to compare pollen rain

spectra with surface sediment pollen samples obtained from the sediment-water interface of five lowland lakes to test the applicability of artificial pollen trap data for comparison with the Quaternary sedimentary record.

The realization of these aims relies strongly on the available floristic datasets recorded in the Salvias Database (2007) for two reasons. First, the inventories provide a target list of reference species from which pollen can be obtained and added to the reference collection held at Edinburgh University, which provides a very detailed collection of taxa obtained from communities situated near fossil pollen sequences in NKMNP. This targeted reference collection not only aids the rapid identification of relevant pollen types found within each of the studied communities and sedimentary records of Laguna Chaplin and Laguna Bella Vista, but it also contains numerous taxa that represent a comprehensive range of vegetation from open savanna through to closed-canopy moist evergreen forest. Indeed, neither the morphological differentiation of key pollen types of the Moraceae family nor the identification of ecosystem specific indicator taxa including *Symmeria*, *Maquira coriacea*, *Anadenanthera* and *Cordia*, would have been possible without such detailed and comprehensive botanical information. Second, floristic data recorded within the Salvias database (2007) were instrumental in determining the extent to which the study plots within NKMNP were representative of rainforest communities across the Amazon Basin. Comparison of these study plots with biometric data obtained from rainforests outside of the park showed that, in general, the rainforests of NKMNP were floristically most similar to those of western Amazonia and least similar to those of the Guiana Shield, which is consistent with the existence of a northeast to southeast Amazonian gradient in tree composition (Ter Steege et al.,

2006; Wittman et al., 2006). *Terra firme* forests of the park exhibit relatively high species richness consistent with those of central Amazonia. Inundated and riparian forest communities in NKMNP exhibit relatively low species richness comparable with similar forests in Southwest Amazonia. Such low species richness may be explained by physiological stresses imposed by a seasonal flooding regime (Nebel et al., 2001; Worbes, 1997; Balslev et al., 1987). The fact that forest communities of NKMNP are floristically comparable with those in southern and western Amazonia lends confidence that their pollen signatures may be compared with fossil pollen records within these regions, especially since only the dominant wind-pollinated trees are well represented in the pollen rain (Chapter 3; Bush and Riviera, 2001).

The differentiation of the four studied rainforest communities also relies on the improved pollen taxonomy of the Moraceae family, one of the most abundant and diverse families growing in tropical rainforests in Southwest Amazonia (Datweiler and Weiblen, 2004; Salvias Database 2007) and the subject of the first aim of this thesis. Descriptive and morphometric analyses on pollen grains of different genera of the family revealed that distinctive pollen types can be recognised. These include *Helicostylis*, a taxon not only well-represented in *terra firme* rainforests of NKMNP but also across the Amazon Basin (VAST, 2007; Fig. 2.6-1); *Brosimum*, of which *B. alicastrum*, *B. lactescens* and *B. guianensis* are late-successional trees and strongly represented in riparian and seasonally flooded forests of lowland Amazonia (VAST, 2007); *B. gaudichaudii*, a common species that grows in dense savanna woodland and upland savannas as well as in seasonally flooded savannahs, both in Bolivia (Killeen 1998; Salvias Database, 2007) and Brazil (De Oliveira-Filho, 1992) ; *Pseudolmedia*, also late-successional canopy trees that grow in both well-drained and

inundated rainforest communities across Amazonia; and *Maquira coriacea*, which is ecologically restricted to riparian evergreen forest communities and similarly found in both blackwater (igapó) and whitewater (várzea) forests across the region (Nebel et al., 2001). The ability to differentiate these grains morphologically, strongly aids the extent to which the four studied rainforest communities may be differentiated by their pollen rain. Indeed different genera of the Moraceae family are key to the palynological separation of *terra firme* rainforest communities from seasonally inundated and riparian forest communities of NKMNP as demonstrated in the ordination analysis of pollen data in chapter 3 (Fig.3.5-4 (e)). In particular, the abundance of *Pseudolmedia*, *Cecropia*, *Pourouma* and *Helicostylis* drives the separation of *terra firme* sites from riparian forest sites, which predominantly comprise *Maquira* and *Brosimum* pollen. Moreover, the abundance of Moraceae pollen in surface sediment samples (Fig. 3.5-2) at Laguna Bella Vista and Laguna Chaplin as well as in lake sediments across Amazonia (Colinvaux et al., 1996; Bush et al., 2004; Haberle and Maslin, 1999), further illustrates the importance of improved pollen taxonomy for their interpretation.

The second and third aims of this thesis were to characterise and differentiate four rainforest communities by their pollen rain and to compare pollen signatures with floral biometric inventories to better understand pollen-vegetation relationships within a rainforest setting. The pollen data obtained from artificial pollen traps within each of the studied forest communities shows that each has a characteristic pollen signature (Fig. 3.5-4 (d and f)). In general, the composition of forest pollen spectra consist of just a few abundant pollen taxa including *Celtis*, *Helicostylis*, *Pseudolmedia*, *Brosimum*, *Maquira* and Melastomataceae/Combretaceae at NKMNP,

and a greater range of less abundant taxa. Of the abundant taxa, wind-pollinated trees are particularly well-represented, which explains not only the widespread abundance of genera of the predominantly anemophilous Moraceae family but also confirms the results of previous studies that show that pollination syndrome strongly affects the composition of the pollen rain of Amazonian rainforest communities (Colinvaux et al., 2000; Bush and Riviera, 2001). The general composition of rainforest pollen assemblages is also mirrored in the floristic datasets where just a handful of tree species dominate in terms of abundance (Salvias Database, 2007; Table 3.5-1). A comparison of pollen and floristic assemblages reveals that many of the dominant trees tend to be prolific pollen producers. This is demonstrated by constrained ordination analysis of pollen and floristic data in chapter three, which showed that the six most significant genera controlling the variance in the pollen data were *Brosimum*, *Maquira*, *Pseudolmedia*, *Celtis*, *Pourouma* and *Tapirira*, each of which is anemophilous and abundant within the floristic inventories. Thus, while much of the floristic detail of the vegetation plots is not represented within their pollen rain, the dominant trees tend to be well represented in both datasets. Hermaphroditic and cleistogamous genera are, by their very nature, less well represented in the pollen rain; however, their presence may be particularly informative when they represent indicator taxa with specific ecological requirements. For example, in NKMNP *Pouteria*, *Cordia*, *Symmeria* and *Sapium* are low pollen producers, but their presence in pollen spectra is diagnostic since *Cordia* is restricted to liana forests, *Pouteria* to flooded forests, and *Symmeria* and *Sapium* to riparian forest communities (Fig. 3.5-2).

The final aim was to compare pollen rain spectra with lake surface sediment pollen assemblages to test the applicability of artificial pollen trap data for comparison with Quaternary lake sedimentary records. Cluster analysis performed on both artificial trap and lake surface samples within NKMNP suggests that their respective pollen spectra are comparable and that differences in the depositional environment (trap samples vs. lake samples) has no real effect on the resulting pollen assemblage (Chapter 3; Fig. 3.5-6 (c)). The closest modern analogue pollen signature to the surface samples at both Laguna Bella Vista and Laguna Chaplin is a riparian forest pollen spectrum; however, significant elements of *terra firme* rainforests are also present, which is consistent with the distribution of forest communities surrounding the lakes today (Fig. 1.6-1). Both trap and lake surface samples of NKMNP are readily differentiated from lake surface samples of gallery forests within the Beni Basin, principally due to the abundance of Poaceae, Cyperaceae and the disturbance indicator *Cecropia* as well as to the absence of pollen types of the Moraceae family in the surface samples of the Llanos de Moxos ecoregion (Beni Basin). These results are consistent with the floristic composition of surrounding vegetation, which is characterised by a low abundance of genera of the Moraceae family and is considerably different to that of riparian forests of NKMNP whose pollen spectra are dominated by Moraceae taxa. In contrast, the pollen signatures at Laguna Huachi, situated within the Madeira-Tapajós moist forest ecoregion, differ from those of liana forests of NKMNP only by the abundance of *Trema* at the site, which is locally abundant along the margins of the lake (Fig. 3.5-6 (e)). Apart from the abundance of this one taxon, the remaining signature closely matches the pollen spectra of *terra firme* moist evergreen and liana forest sites in NKMNP. Therefore,

not only do these data demonstrate that the pollen rain sampled from artificial pollen traps may be directly compared with lake surface sample records, since similar trap and surface sediment spectra of NKMNP plot together in ordination analysis, but they also indicate that the spectra are applicable to sites outwith the park within the Madeira-Tapajós moist forest ecoregion, but not to gallery forests of the Beni Basin (Llanos de Moxos ecoregion).

4.3 Wider implications

4.3.1 *Palaeoenvironmental implications*

The extent to which the pollen spectra obtained in NKMNP may be applicable to fossil pollen records outside the study area requires further study. Nevertheless, chapter two demonstrates that the studied Moraceae taxa are widely distributed across the Amazon Basin (Fig. 2.6-1), indicating that such improved taxonomic resolution of pollen types of the Moraceae family may indeed be relevant for improved interpretation of palaeoecological records elsewhere in the region. Moreover, many rainforest pollen assemblages obtained from sedimentary records across the Amazon Basin show remarkable similarity to those of NKMNP, in particular to the riparian forest signature. For example, pollen assemblages obtained from Holocene lake sediments at Lago Tapajós situated within the Madeira-Tapajós moist forest ecoregion in eastern Amazonia, share very similar characteristics to riparian forests at NKMNP (Irion et al., 2006). Early Holocene pollen assemblages deposited during the initial formation of the lake were interpreted by the authors as representing closed-canopy lowland forest characteristic of both riparian forest and *terra firme* elements. The *terra firme* elements, however, comprised the following

taxa: *Alchornea*, *Brosimum*, *Pouteria*, *Sapium*, *Sebastiana*, *Socratea*, *Symmeria* and *Waltheria*. When compared with pollen signatures obtained from lowland forests at NKMNP, it is clear that this combination of taxa actually reflects riparian forest communities and on this basis alone there is no palynological evidence to support the presence of *terra firme* rainforest during the Holocene at this site. While absence of pollen spectra characteristic of *terra firme* rainforests does not necessarily mean absence of *terra firme* rainforest *per se*, it is clear that the sediments of Rio Tapajós only record pollen spectra of forest communities lining the Tapajós River and the site cannot therefore be invoked to support the presence of spatially extensive closed canopy rainforest communities during the early Holocene period.

The potential applicability of the results for the interpretation of Quaternary vegetation records elsewhere in Amazonia is therefore clear. Indeed, if pollen assemblages of Lago Tapajos in Eastern Amazonia are similar to those within NKMNP then these results may also be of particular importance for the interpretation of glacial fossil pollen assemblages recorded in sediments of the Amazon Fan (Haberle 1997; Haberle and Maslin, 1999). Moreover, a reassessment of the pollen record at this site may help resolve much of the controversy surrounding the Quaternary vegetation dynamics of Amazonia's rainforests. The persistent abundance of Moraceae/Urticaceae pollen in the sedimentary record of the Amazon Fan throughout the last glacial-Holocene sequence is suggested by some to indicate that the Amazon Basin was covered by extensive rainforest throughout this period (e.g. Haberle and Maslin; Colinvaux *et al.*, 2000; Bush *et al.*, 2004). Others have suggested its presence may simply reflect gallery or riparian forests lining the rivers during glacial periods, which masked pollen from savannahs or dry forests beyond,

consistent with the glacial aridity hypothesis (Haffer, 1969; Haffer and Prance, 2001; Prado and Gibbs, 1993; Pennington *et al.*, 2000; Van der Hammen and Absy, 1994). Improvements in the pollen taxonomy of the Moraceae family and the characterisation of rainforest communities in NKMNP demonstrates that riparian and *terra firme* rainforests can be differentiated from each other palynologically and may therefore help determine the exact nature of the rainforest pollen signal within the Amazon Fan record. If the Moraceae/Urticaceae curve comprised *Helicostylis* pollen and was further associated with taxa indicative of well-drained conditions such as *Celtis* and *Cordia*, this would provide strong support for the presence of spatially extensive *terra firme* rainforests distant from the river courses and the continuous forest hypothesis (Colinvaux et al., 1996) since these taxa are ecologically restricted to *terra firme* plant communities in NKMNP. If, however, the Moraceae/Urticaceae pollen signal was found to comprise riparian indicator taxa such as *Maquira* or *Brosimum*, as well as indicator taxa from other families such as *Symmeria* and *Sapium* then this would suggest the Amazon Fan sediments record a predominantly riparian signal consistent with the glacial aridity hypothesis (Haffer, 1969; Prado and Gibbs, 1993; Haffer and Prance, 2001; Pennington et al. 2000).

4.3.2 *Underlying Assumptions*

One fundamental assumption inherent within this thesis is that the studied one hectare plots are considered to be representative of larger homogeneous rainforest populations (plant communities) both within and, to a lesser extent, outwith NKMNP. Attempts to classify vegetation groups into plant communities or by their pollen signatures, inevitably places any given study within the remit of

Phytosociology, the study of characteristics, classification, relationships and distribution of plant communities (Kent and Coker, 1996). By their very nature, phytosociological studies adopt, to a considerable extent, the views of Clements (1916, 1928) on the existence of the plant community and its repeatability through space. Such a view is not without criticism and contrasts with an alternative individualistic view of plant associations, which asserts that plant associations represent a snap-shot of vegetation change through space and time and that their classification is therefore less meaningful. While plant communities may exist at any given point in space and time, they are merely random associations and are not spatially consistent across any given region (Gleason, 1917, 1926, 1939). The occurrence of glacial and Late-glacial fossil pollen spectra with no known modern analogues in both high (See for example Anderson 1989; Williams et al., 2001; Birks 2003) and low latitudes (Colinvaux et al., 1996; Bush et al., 2004; Haberle and Maslin, 1999) lends further support for Gleason's (1939) individualistic concept of the nature of vegetation (Birks and Gordon, 1985). Furthermore, this individualistic stance has gained recent support through the application of the phenomenon of 'self-similarity' to vegetation studies, which asserts that discreet communities do not exist and that patterns of heterogeneity are independent of the spatial scale at which observation is made i.e. that β-diversity (between-habitat diversity) and α-diversity (across-habitat diversity) are indistinguishable (Wilson and Chiarucci, 2000, 2001).

While accepting the growing support for an individualistic view of the nature of vegetation dynamics, a strong case for the subdivision of the vegetation of NKMNP into plant communities can still be made. The distinctiveness of these plant communities may be defended since species turnover (β-diversity) has been well-

documented in the park through the analysis of Landsat^{TM} satellite images as well as of botanical inventories recovered from 32 permanent vegetation plots representing each of the inferred vegetation formations (Killeen, 1998; Salvias Database, 2007). The distribution of plant communities is strongly controlled by edaphic and geomorphological constraints that provide considerable substrate heterogeneity but restrict the ability of given community to become spatially extensive.

The extent to which studied plots are representative of larger homogeneous rainforest populations outside the park is, however, more difficult to assess. A strong case can be made to show that riparian and seasonally inundated plots of NKMNP are indeed representative of floodplain forests elsewhere in Southwest Amazonia, since much of the vegetation is specialised and adapted to grow on hydromorphic Entisols within a hydrologically constrained environment. The interconnectedness of Amazonian fluvial systems provides a direct vector along which plant communities can become readily established lining watercourses that traverse a considerable geographic area. The probability, therefore, that such communities are floristically similar to others across large spatial scales is arguably quite high. Indeed, distinct riparian vegetation types are recognised throughout Amazonia (Anderson, 1981; Pires and Prance, 1985; Kahn and Mejia, 1990; Duque et al. 2002). Since many riparian species are indicator species, including amongst others *Maquira coriacea* (Nebel et al., 2001) and *Symmeria paniculata* (Ferreira and Stohlgren, 1999), whose pollen is well-represented in the pollen rain, there is considerable potential for the application of riparian forest pollen signatures to key fossil pollen sites across Amazonia; for example, sediments of the Amazon Fan (Haberle, 1997; Haberle and Maslin, 1999) and those of Rio Tapajós (Irion et al., 2006).

While hydrologically determined vegetation types of NKMNP may be representative of similar communities outside the park for the reasons given above, the same cannot necessarily be said for *terra-firme* communities. In contrast to substrate-controlled *terra firme* rainforest communities of NKMNP, other Amazonian *terra firme* forests generally grow on homogeneous substrates that are spatially more extensive than in NKMNP. These forests exhibit low species turnover (β-diversity) over large areas restricted by the limits imposed by plant dispersal mechanism rather than heterogeneity of substrate (Condit et al., 2002; Duivenvoorden et al., 2002; Phillips et al., 2003). The *terra firme* forests of NKMNP and the dispersal-limited *terra firme* forests of central Amazonia are therefore less likely to share the same taxonomic composition. It follows that the floristic composition of geomorphically controlled *terra firme* plots in NKMNP is less likely to be representative of *terra firme* forest communities elsewhere in Amazonia.

Nevertheless, from a palynological standpoint this may be less of a problem since there is evidence to suggest that a small group of dominant tree species are able to inhabit *terra firme* forests of Amazonia regardless of substrate heterogeneity or dispersal mechanism (Pitman et al. 1999, 2001; Phillips et al. 2003). It is generally these dominant tree species that exhibit anemophilous pollination syndromes (Fig. 3.5-5 (e,f); Table 3.5-1) and are therefore well represented in pollen assemblages. Since the subtle floristic differences revealed across extensive areas of *terra firme* rainforest (Ter Steege et al., 2006; Witman et al., 2006) are unlikely to be picked up by the pollen rain, which is dominated by pollen of the dominant and abundant tree species, then the pollen rain of *terra firme* forests in NKMNP may be representative

of that elsewhere in the Amazon Basin. Further study is required to confirm this testable hypothesis.

The second assumption underpinning this thesis relates to the comparison of modern analogue pollen signatures to the fossil pollen record (Chapter 3). The process of 'analogue matching' assumes that the relationships between modern plant communities and their pollen rain are the same as those between past communities and fossil pollen spectra (Jackson and Williams, 2004). However, a number of factors complicate these relationships including differences/changes in the pollen-depositional environment, contemporary anthropogenic influences on floristic composition of plant communities, the dispersal of the same pollen spectrum by different plant communities (convergence) and conversely, the production of different spectra from the same community (divergence) (Birks and Gordon, 1985). The potential occurrence of non-analogue communities in the past further restricts the applicability of the modern analogue technique. There are numerous examples of these during glacial age, Lateglacial and early Holocene times in both high and low latitudes. For example, non-analogue pollen spectra are found within sedimentary records of Eastern North America between 17-12000 ^{14}C yr BP and 14000-9000 ^{14}Cyr BP, which brackets times of extensive climatic change in the region (Williams et al. 2001). In northern Europe, Lateglacial climate was affected by the proximity of large ice sheets and characteristic vegetation comprised trees exhibiting low pollen productivity, which enabled pollen that was transported over long distances to become well represented within the sedimentary record (Birks, 2003). The geographic distribution of source areas was quite different to that of today resulting in pollen assemblages with no contemporary analogue. In tropical South America,

non-analogue pollen assemblages are found in most of the glacial sedimentary records including Lake Pata (Colinvaux et al., 1996), Laguna Bella Vista and Laguna Chaplin (Mayle et al., 2000; Burbridge et al., 2004), the oceanic sediments of the Amazon Fan (Haberle 1997; Haberle and Maslin, 1999), lakes San Juan Bosco (Bush et al., 1990) and Mera (Liu and Colinvaux, 1985) and at Lake Carajas (Absy et al., 1991). Most of these records show an increased abundance of Andean taxa *Podocarpus*, *Drymis* and *Alnus* pollen within glacial sediments, interpreted as being the individualistic response of temperature sensitive taxa to lower temperatures and their incorporation into tropical lowland forests (Colinvaux et al., 2000). At Lake Carajas, *Ilex* pollen is prominent in glacial sediments but entirely disappears in the Holocene record and is similarly interpreted as individualistic migration of this taxon from lowland forests into more elevated vegetation associations in the Andes due to Holocene warming (Absy et al., 1991).

Despite the above complications, the application of the modern analogue technique is generally considered to be robust during the last 6000 to 9000 years of the Holocene (Birks and Gordon, 1985; Jackson and Williams, 2004), which is confirmed by the comparison of the results of analogue matching with other palynological as well as plant-macrofossil analyses (Birks, 2003; Jackson et al.1997). The temporal constancy of pollen records of the Amazon Basin (Haberle and Maslin, 1999; Colinvaux et al. 1996, Irion et al., 2006) throughout the Holocene also suggests that little structural and/or floristic changes took place over this period and that the represented vegetation is similar to that of today. Furthermore, contemporary Amazonia, and indeed NKMNP, is globally unique by virtue of the availability of 'pristine' vegetation for scientific research. This lends confidence that modern plant

communities in the region represent relatively undisturbed, 'natural' vegetation whose signatures are more applicable for analogue matching with the fossil pollen record when compared with high latitude equivalents such as Europe and North America where little natural vegetation remains due to anthropogenic activity. It seems reasonable to assume, therefore that modern analogue signatures obtained from pristine plant communities of the Amazon Basin may confidently be 'matched' with fossil pollen assemblages of the Holocene sedimentary record. The comparison of modern analogue pollen spectra with those found in Glacial and Lateglacial sediments should, however, be performed with caution; nevertheless, since the technique utilises relative dissimilarity measures, considerable palaeoecological information may still be extracted regarding the extent to which past (non-analogue) communities are similar/different to those of today.

4.3.3 *Future Research*

This final section discusses some potential implications of the results presented in this thesis for the development of palynological studies in lowland Amazonia. Since the comparison of artificial trap and surface sample pollen assemblages has been shown to be applicable within NKMNP (Chapter 3) and that anthropogenic activity has had comparatively little effect on the composition of modern plant communities within the park, it would be fruitful to adopt the modern analogue approach of Overpeck et al. (1985) and Guiot (1990) and establish a database of modern analogue pollen signatures representing the full spectrum of plant communities in NKMNP. Development of such a database is in progress and will include pollen spectra of rainforest communities studied here as well as those obtained from the full range of

terra firme and seasonally inundated savanna and semi-deciduous dry forest communities (Gosling, 2004; Jones and Mayle, pers com; Gosling et al., 2005). Once complete, it will provide the first comprehensive collection of Amazonian pollen signatures to which fossil pollen records of Laguna Bella Vista and Laguna Chaplin will be numerically compared. Such comparisons may be made using multivariate ordination and cluster analyses of both modern and fossil pollen spectra as demonstrated in chapter 3 and will provide a clear indicator of the degree of similarity between them. Threshold similarity values will be set so that particular fossil pollen assemblages may be clearly assigned to a given modern analogue spectrum (Overpeck and Webb, 1983; Birks and Gordon, 1985). The detection of no-modern analogue communities is also readily observed within a multivariate ordination analysis when fossil pollen spectra cluster separately from the modern analogue spectra. Extension of the database to include pollen signatures of plant communities across southwestern Amazonia is envisaged when further modern pollen studies are performed within pre-existing networks of vegetation plots such as those set up by the Tropical Biomes in Transition consortium (TROBIT, 2007) and the Amazon Forest Inventory Network (Peacock et al., 2007). Moreover, many of these plots have climate data associated with them permitting the regional distribution of modern pollen spectra to be compared with climate data, which in turn, will provide the means to obtain regional climate reconstructions through the development of pollen-based transfer functions. Similar pollen-based climate reconstructions have been performed successfully using a pollen-based transfer function approach in eastern North America (Webb et al., 1993), northern Europe (Seppa et al., 2004) and New Zealand (Wilmshurst et al., 2007). Since much of the

vegetation in Amazonia still remains in a pristine condition, pollen-based climate reconstructions are likely to exhibit comparatively small error margins when compared with these studies since the modern analogue pollen spectra of the latter are strongly affected by anthropogenic activity such as deforestation and agricultural landuse (Wilmshurst et al., 2007).

Rainforests of the Amazon Basin account for around 10% of the world's primary productivity and carbon storage in terrestrial ecosystems (Mellilo *et al.*, 1993; Tian *et al.*, 1998). Until now, our inability to distinguish Amazonian forest pollen spectra from each other has resulted in low resolution, biome-scale estimates of past carbon storage (Behling 2002). An improved understanding of Quaternary rainforest dynamics should also help provide more precise estimates of past carbon storage, which will provide an important contribution to our understanding of the global carbon cycle and enable a more precise estimation of past carbon sequestration. If the heterogeneity exhibited by rainforest communities can be mirrored by pollen assemblages obtained from across the Amazon Basin, then there is considerable scope to not only provide greater precision in the estimation of past carbon storage, but also to provide empirical data to better constrain earth system models (Valdes, 2000; Cowling *et al.*, 2006). Furthermore, pollen rain studies in rainforest settings (e.g.Vincens *et al.*, 2000) have revealed a correlation between pollen deposition and leaf area index (LAI; the cumulative leaf area above ground per unit area of ground surface). LAI is sensitive to climate and atmospheric CO_2 (Chase *et al.*, 1996; Cowling *et al.*, 1999) and has been used as a proxy for canopy density. If the correlation between pollen deposition and inundation gradient exhibited by rainforest communities at NKMNP is further correlated with LAI (a

reasonable contention considering the structural differences between these forest communities) then it follows that pollen influx may be used as a proxy for LAI. Consequently, LAI may be directly estimated from the fossil pollen record and applied to better test earth-system palaeomodels (e.g. Cowling *et al.*, 1999, 2006; Valdes, 2000). Further study is therefore required to test the correlation between LAI and pollen deposition along inundation gradients within rainforest ecosystems.

The interpretation of Amazonian fossil pollen diagrams may be further improved by the modelling of pollen dispersal and deposition and simulation of pollen source area for the diverse plant communities of NKMNP. Modelling studies hold considerable promise for the development of robust methods to infer past changes in land cover and floristic diversity from fossil pollen data (Bunting et al., 2004). Considerable progress had been made in this field in Northern Europe where the complexity associated with different pollen dispersal mechanisms has been investigated by members of the pollen/landscape calibration network (Pollandcal) using models of pollen dispersal and deposition (Prentice, 1985; Sugita, 1994; Sugita et al., 1999; Bunting et al., 2004; Bunting et al., 2005; Bunting and Middleton, 2005). Moreover, simulation approaches have been adopted to explore the effect of variation in landscape patterns and taxon parameters such as pollen productivity and fall speed on the pollen source area (Bunting et al., 2004). These simulations indicate that the relevant pollen source area may be calculated for a given environmental setting, but is strongly affected by temporal changes in the spatial distribution of plant communities. The taphonomic processes that govern pollen deposition in the Amazonian lowlands are inherently different to those in Northern Europe due to enhanced pollen transport through complex hydrological networks; however,

considerable scope exists to adapt such models to incorporate alternative dispersal and deposition algorithms. Indeed, the development of HUMPOL software (Bunting and Middleton, 2005) permits the development of alternative models of pollen dispersal in different environmental settings and would provide an ideal springboard for such research in the Amazon Basin.

4.4 References

Absy, M. L., Cleef, A., Fornier, M., Servant, M., Siffedine, A., Da Silva, M. F., Soubies, F., Suguio, K., Turcq, B., and Van der Hammen, T. (1991). Mise en evidence de quatre phases d'ouverture dela forêt dense le sud-est de l'Amazonie au cours des 60 000 dernières années. Premiere comparaison avec d'autres régions tropicales. *C.R. Acad.Sci.Paris.* **313**, 673-678.

Anderson, A. B. (1981). White-sand vegetation of Brazilian Amazonia. *Biotropica* **13**, 199-210.

Anderson, P. M., Bartlein, P. J., Brubaker, L. B., Gajewski, K., and Ritchie, J. C. (1989). Modern analogs of Late Quaternary pollen spectra from the western interior of North America. *Journal Of Biogeography* **16**, 573-596.

Balslev, H., Lutteyn, J., Yllgaard, B., and Holm-Nielsen, L. (1987). Composition and structure of adjacent unflooded and floodplain forest in Amazonian forests. *Botanical Gazette* **111**, 413-425.

Behling, H. (2002). carbon storage increases by major forest ecosystems in tropical South America since the Last Glacial Maximum and the early Holocene. *Global And Planetary Change* **33**, 107-116.

Birks, H. H. (2003). The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. *Quaternary Science Reviews* **22**, 453-473.

Birks, H. J. B., and Gordon, A. D. (1985). *Numerical Methods in Quaternary Pollen Analysis*. Academic Press: London.

Bunting, M. J., Armitage, R. A., Binney, H. A., and Waller, M. P. (2005). Estimates of 'relative pollen productivity' and 'relevant source area of pollen' for major tree taxa in two Norfolk (UK) woodlands. *The Holocene* **15**, 459-465.

Bunting, M. J., Gaillard, M. J., Sugita, S., Middleton, R., and Brostrom, A. (2004). Vegetation structure and pollen source area. *The Holocene* **14**, 651-660.

Bunting, M. J., and Middleton, D. (2005). Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology* **134**, 185-196.

Bush, M., Weimann, M., Piperno, D. R., and Liu, K. B. (1990). Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Research* **34**, 330-345.

Bush, M. B., De Oliveira, P. E., Colinvaux, P. A., Miller, M. C., and Moreno, J. E. (2004). Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214**, 359.

Bush, M. B., and Rivera, R. (2001). Reproductive ecology and pollen representation among neotropical trees. *Global Ecology and Biogeography* **10**, 359-367.

Chase, T. N., Pielke, R. A., Kittel, T. G. F., Nemani, R. R., and Running, S. W. (1996). Sensitivity of a general circulation model to global changes in leaf area index. *Journal of Geophysical Research* **101,** 7393-7408.

Clements, F. E. (1916). *Plant Succession. An analysis of the development of vegetation.* Carnegie Institute, Washington D.C.

Clements, F. E. (1928). *Plant Succession and Indicators.* H.W. Wilson, New York.

Colinvaux, P. A., De Oliveira, P. E., and Bush, M. B. (2000). Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19**, 141-169.

Colinvaux, P. A., DeOliveira, P. E., Moreno, J. E., Miller, M. C., and Bush, M. B. (1996). A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* **274**, 85-88.

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., and Foster, R. B. (2002). Beta-diversity in tropical forest trees. *Science* **295**, 666-669.

Cowling, S. A. (1999). Simulated effects of low atmospheric CO2 on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecology and Biogeography* **8**, 81-93.

Cowling, S. A., and Shin, Y. (2006). Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO_2 within a region of Amazonia. *Global Ecology and Biogeography* **15**, 553-566.

Datwyler, S. L., and Weiblen, G. D. (2004). On the origin of the fig: Phylogenetic relationships of Moraceae from ndhF sequences. *American Journal of Botany* **91**, 767-777.

de Oliveira-Filho, A. T. (1992). The vegetation of Brazilian 'murundus' – the island-effect on the plant community. *Journal of Tropical Ecology* **8**, 465-486.

Duivenvoorden, J., Svenning, J. C., and Wright, S. J. (2002). Beta diversity in tropical forests. *Science* **295**, 636-647.

Duque, A., Sanchez, M., Cavelier, J., and Duivenvoorden, J. (2002). Different floristic patterns of woody understory and canopy plants in Columbian Amazonia. *Journal Of Tropical Ecology* **18**, 499-525.

Ferreira, L. V., and Stohlgren, T. J. (1999). Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia* **120**, 582-587.

Gleason, H. A. (1917). The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* **43,** 463-481.

Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**, 1-20.

Gleason, H. A. (1939). The individualistic concept of the plant association. *American Midland Naturalist* **21**, 92-110.

Gosling, W. D. (2004). Characterization of Neotropical forest and Savannah Ecosystems by their Modern Pollen Spectra. Unpublished PhD Thesis. University of Leicester.

Gosling, W. D., Mayle, F. E., Tate, N. J., and Killeen, T. J. (2005). Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research* **64**, 284-297.

Guiot, J. (1990). Methodology of the last climatic cycle reconstruction in France from pollen data. *Palaeogeography Palaeoclimatology Palaeoecology* **80**, 49-69.

Haberle, S. (1997). Upper Quaternary Vegetation and climate history of the Amazon Basin: correlating marine and terrestrial pollen records. In "Proceedings of the Ocean Drilling Program, Scientific Results." (R. D. Flood, D. J. W. Piper, A. Klaus, and L. C. Peterson, Eds.), pp. 381-396. Ocean Drilling Program, College Station, TX.

Haberle, S. G., and Maslin, M. A. (1999). Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon fan, ODP site 932. *Quaternary Research* **51**, 27-38.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165**, 131-137.

Haffer, J., and Prance, G. T. (2001). Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* **16**, 579-607.

Irion, G., Bush, M. B., de Mello, J. A. N., Stuben, D., Neumann, T., Muller, G., De, J. O., and Junk, J. W. (2006). A multiproxy palaeoecological record of Holocene lake

sediments from the Rio Tapajós, eastern Amazonia. *Palaeogeography Palaeoclimatology Palaeoecology* **240**, 523-535.

Jackson, S. T., Overpeck, J. T., Webb, T., Keattch, S. E., and Anderson, K. H. (1997). Mapped plant macrofossil and pollen records of late Quaternary vegetation change in eastern North America. *Quaternary Science Reviews* **16**, 1-70.

Jackson, S. T., and Williams, J. W. (2004). Modern analogs in Quaternary Paleoecology: Here today, Gone Yesterday, Gone Tomorrow? *Annual reviews of Earth and Planetary Sciences* **32**, 495-537.

Kahn, F., and Mejia, K. (1990). Palm communities in wetland forest ecosystems of Peruvian Amazonia. *Forest Ecology and Management* **33**, 169-179.

Killeen, T. J. (1998). "Vegetation and flora of Noel Kempff Mercado National Park." Conservation International, Washington, DC.

Liu, K. B., and Colinvaux, P. A. (1985). Forest changes in the Amazon basin during the last glacial maximum. *Nature* **318**, 556-557.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., and Schloss, A. L. (1993). Global Climate-Change and Terrestrial Net Primary Production. *Nature* **363**, 234-240.

Nebel, G., Dragsted, J., Simonsen, T. R., and Vanclay, J. K. (2001a). The Amazon flood plain forest tree Maquira coriacea (Karsten) CC Berg: aspects of ecology and management. *Forest Ecology and Management* **150**, 103-113.

Nebel, G., Kvist, L. P., Vanclay, J. K., Christensen, H., Freitas, L., and Ruiz, J. (2001b). Structure and floristic composition of flood plain forests in the Peruvian Amazon I. Overstorey. *Forest Ecology and Management* **150**, 27-57.

Overpeck, J. T., and Webb, T. (1983). Calibration of numerical dissimilarity measures for matching modern and fossil pollen spectra. *Bulletin of the Ecological Society of America* **64**, 155.

Overpeck, J. T., Webb, T., and Prentice, I. C. (1985). Quantitative Interpretation Of Fossil Pollen Spectra - Dissimilarity Coefficients And The Method Of Modern Analogs. *Quaternary Research* **23**, 87-108.

Peacock, J., Baker, T. R., Lewis, S. L., Lopez-Gonzales, G., and Phillips, O. (2007). The RAINFOR database: Monitoring forest biomass and dynamics. *Journal of Vegetation Science* **18**, 535-542.

Pennington, R. T., Prado, D. E., and Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal Of Biogeography* **27**, 261-273.

Phillips, O., Nunez-Vargas, P., Monteagudo, A. L., Cruz, A. P., Zans, M. C., Sanchez, W. G., Yli-Halla, M., and Rose, S. (2003). Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* **91**, 757-775.

Pires, J. M., and Prance, G. T. (1985). The vegetation types of the Brazilian Amazon. In "Key Environments: Amazonia." (G. T. Prance, and T. E. Lovejoy, Eds.), pp. 109-145. Pergamon, Oxford.

Pitman, N. C., Terborgh, J., Silman, M. R., Nunez, P. V., Neill, D., and Ceron, C. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**, 2101-2117.

Pitman, N. C., Terborgh, J., Silman, M. R., and P.V., N. (1999). Tree species distributions in an upper Amazonian forest. *Ecology* **80**, 2651-2661.

Prado, D. E., and Gibbs, P. E. (1993). Patterns of species distribution in the seasonally dry forests of South America. *Annals of the Missouri Botanical Gardens* **80**, 902-927.

Prentice, I. C. (1985). Pollen Representation, Source Area, And Basin Size - Toward A Unified Theory Of Pollen Analysis. *Quaternary Research* **23**, 76-86.

Seppa, H., Birks, H. J. B., Odland, A., Poska, A., and Veski, S. (2004). A modern pollen-climate calibration set from northern Europe: developing and testing a tool for palaeoclimatological reconstructions. *Journal Of Biogeography* **31**, 251-267.

Sugita, S. (1994). Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology* **82**, 881-897.

Sugita, S., Gaillard, M. J., and Brostrom, A. (1999). Landscape openness and pollen records: a simulation approach. *The Holocene* **9**, 409-421.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J. F., Prevost, M. F., Spichiger, R., Castellanos, H., von Hildebrand, P., and Vasquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**, 444-447.

Tian, H. Q., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich, J. V. K., Moore, B., and Vorosmarty, C. J. (1998). Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**, 664-667.

Valdes, P. J. (2000). South American palaeoclimate model simulations: how reliable are the models? *Journal Of Quaternary Science* **15**, 357-368.

Van der Hammen, T., and Absy, M. L. (1994). Amazonia During the Last Glacial. *Palaeogeography Palaeoclimatology Palaeoecology* **109**, 247-261.

Vincens, A., Dubois, M. A., Guillet, B., Achoundong, G., Buchet, G., Beyala, V. K. K., de Namur, C., and Riera, B. (2000). Pollen-rain-vegetation relationships along a forest-savanna transect in southeastern Cameroon. *Review Of Palaeobotany And Palynology* **110**, 191-208.

Webb, R. S., Anderson, K. H., and Webb, T. (1993). Pollen response surface estimates of late Quaternary changes in the moisture balance of the northeastern United States. *Quaternary Research* **40**, 213-227.

Williams, J. W., Bartlein, P. J., and Webb, T. (2001). Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* **82**, 3346-3362.

Wilmshurst, J. M., McGlone, M. S., Leathwick, J. R., and Newnham, R. M. (2007). A pre-deforestation pollen-climate calibration model for New Zealand and quantitative temperature reconstructions for the past 18000 years BP. *Journal Of Quaternary Science* **22**, 535-547.

Wilson, J. B., and Chiarucci, A. (2000). Do plant communities exist? Evidence from scaling-up local species-area relations to the regional level. *Journal of Vegetation Science* **11**, 773-775.

Wilson, J. B., and Chiarucci, A. (2001). self-similarity and Phantoms: A response to Hill. *Journal of Vegetation Science* **12**, 299.

Wittmann, F., Schongart, J., Montero, J. C., Motzer, T., Junk, W. J., Piedade, M. T. F., Queiroz, H. L., and Worbes, M. (2006). Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* **33**, 1334-1347.

Worbes, M. (1997). *The forest ecosystem of the floodplains.* In "The central Amazon floodplain: ecology of a pulsating system." (W. J. Junk, Ed.), pp. 223-265. Springer, Berlin.